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EFFECTS OF CATTLE GRAZING ON THE MOUNTAIN PARKLAND ECOSYSTEM, MAUNA LOA, HAWAII

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LITERATURE REVIEW

The objective of this investigation is to determine the effects that cattle have had on vegetation and soils of the mountain parkland ecosystem of Mauna Loa on the island of Hawai'i. A portion of this ecosystem is contained within Hawaii Volcanoes National Park and has been protected from cattle grazing since 1948. The mountain parkland ecosystem extends from the Park into neighboring ranchlands, where cattle grazing continues. In this study, grass and shrub communities of this ecosystem in the Park were compared with corresponding communities of the adjacent ranch. Differences in vegetation and species composition were quantified, and various soil parameters were examined to determine whether edaphic factors differed in the two areas.

As the Hawaiian Islands support no indigenous mammal species other than the hoary bat (Lasiurus cinereus) and the monk seal Monachus schauinslandi (Tomich 1969), the mountain parkland ecosystem and all other Hawaiian land ecosystems evolved in the absence of large herbivores (plant-eating animals). Thus the Hawaiian flora has not undergone selection for resistance to herbivory. The introduction of large mammals began at the end of the 18th century and has included cattle (Bos taurus), sheep (Ovis aries and O. musimon), goats (Capra hircus), deer (Axis axis and Odocoileus hemionus), and pigs (Sus scrofa).

The purpose of this literature review is to ascertain how cattle and other large mammalian herbivores have affected natural vegetation in various parts of the world. Ecosystems with indigenous mammalian herbivores and those which have evolved in the absence of large animals are considered for the purpose of determining whether the two types of ecosystems are differently affected by herbivores. These examples of herbivory in other parts of the world may lend insight to the impact of introduced animals in the mountain parkland of Mauna Loa as well as in other parts of the Hawaiian Islands.

Effects of Grazing

Grazing by any large mammalian herbivore has the obvious effect of removal of biomass from plants in the community. Some writers have claimed that grazing may actually benefit the vegetation of an area (Weaver & Rowland 1952, Kelting 1954, Duvall 1962, Reardon & Merrill 1976). Ellison (1960) summarized the supposed benefits as a stimulation of herbage production, increased drought resistance, mulch removal, transportation and planting of seeds, formation of trails that check the flow of water downslope, and fertilization of soil. However, in Ellison's opinion, there was no real evidence to support these claims for beneficial effects of grazing on vegetation.

Another view held by many writers is that only overgrazing has a deleterious effect on vegetation (Humphrey 1962). Some results of overgrazing are an alteration of species composition with extinction of palatable plants, thinning of vegetation cover, trampling of soil, soil erosion, and invasion of shrubby or weedy species (Stoddart & Smith 1943). The distinction between overgrazing and simple grazing may be quite subjective and varies with the author and ecosystem.

Ares and Leon (1972) state that grazing can be a factor limiting stability through the removal of biomass. There is speculation that the world's grasslands may not be climatic climaxes, but rather in a state controlled in part by biotic factors including grazing (Moore 1966).

A factor in any consideration of effects of grazing on vegetation is the species of herbivore involved. Various herbivores, including domestic livestock, have preferences for different types of food plants (i.e., grasses, forbs or woody plants) and may affect the same type of vegetation differently due to dissimilarities in the mechanics of feeding behavior.

Grazing by large herbivores may affect the soil, plant, and animal components of an ecosystem. Herbivores may alter both the species composition and structure of the natural vegetation of an area. Specific examples of such effects of grazing are considered in the following sections.

Influence of Cattle on Vegetation

Cattle are among the most important large herbivores of the western world from an economic standpoint; they have accordingly stimulated a large number of studies, as well as texts on range management and effects of grazing on pasture conditions. An early reference to the visible effect of domestic cattle on vegetation occurs in one of Darwin's Journals (Darwin 1839). While on a trip through the pampas of Argentina, Darwin noticed a marked change in vegetation cover on opposing sides of a river. Due to cattle grazing, natural vegetation changed from "coarse herbage to a carpet of fine green verdure."

Since Darwin's time many studies have been carried out to determine specific effects of livestock grazing. Many American authors have reported that cattle grazing may result in indigenous grasses being replaced by forbs (Weaver & Albertson 1940; Weaver & Darland 1948; Colman 1953). Such changes may occur in short-grass areas and bunchgrass regions under heavy grazing (Stoddart & Smith 1943). Livestock grazing in lower elevation grasslands of southwestern Idaho have had the effect of replacing the native bunchgrass, wheatgrass (Agropyron sp.), with cheatgrass (Bromus secalinus), an introduced annual (Colman 1953).

Using exclosures, Weaver and Darland (1948) found that heavy grazing by cattle resulted in degeneration of the bluestem (Andropogon gerardi) prairie of Nebraska to a community in which native prairie grasses and forbs were rare. Unpalatable species, non-native weeds, and some native shrubs increased under grazing.

Another commonly reported effect of grazing is a change in vegetation structure of an area. Desert grassland of the southwestern United States may be invaded by shrub-oak (Quercus sp.) and mesquite (Prosopis sp.) as a result of overgrazing. Replacement of perennial grasses by annual species may accompany this invasion (Stoddart & Smith 1943). In a long-term study of fescue (Festuca spp.) grasslands in western Canada, the dominant grass species (Festuca scabrella) was replaced by Danthonia parryi and quaking aspen (Populus tremuloides) encroached upon moderately grazed fields (Johnston 1971). Cooper (1960) described the stages involved in replacement of native grasses in northern Arizona under heavy grazing. The native tall-bunchgrasses were first replaced by more resistant species and mid-grasses were replaced by short-grasses. If grazing continued, even the short-grasses were replaced by perennial and annual forbs. Grazing also led to an increase in cover of pines (Pinus sp.).

A similar effect of grazing (or overgrazing) was reported in the Midwest (Weaver & Albertson 1940). Here a mixed prairie was converted into a short-grass plain, and many native forbs disappeared. Bare soil was exposed and annuals and cactus invaded.

Grazing also affects the physical and chemical properties of soils. Johnston et al. (1971) found that cattle grazing in fescue grasslands of Canada resulted in lower percentages of organic matter, percentage phosporus, and soil moisture, while soil pH and soil temperature increased. A study carried out in South Dakota had similar results (Beebe & Hoffman 1963). Overgrazing also decreased the nitrogen content in the upper layers of the soil. Along the same lines, Leaf (1958) found that grazing decreased levels of nitrogen and other nutrients in woodlot soils. Two physical properties of soils which are often examined in grazing studies are soil moisture content and bulk density. Johnston (1962) reported that both the percentage soil moisture and water-intake rate of fescue grassland soils decreased under any intensity of grazing. Other authors (Ellison 1960; Linnartz et al. 1966; Adams 1975; McCarty & Mazurak 1976) have presented evidence linking the trampling effect of cattle with an increased soil bulk density through compaction.

Some of the most meaningful studies of cattle grazing concern a comparison of grazed and ungrazed areas. One such study in Oklahoma compared four plots: protected prairie, grazed prairie, protected former cropland, and grazed former cropland (Penfound 1964). This area was originally a tall-grass prairie but had been moderately grazed for many years. After 13 years

the dominant plant in the prairie plots (Andropogon scoparius, little bluestem grass) remained the same in the grazed area, while in protected prairie the mid-grasses present in the beginning were partially replaced by tall-grasses and native woody plants. The vegetation of grazed cropland changed from annual grasses to short-grasses and mid-grasses and then to mid-grasses alone. In the same interval, protected cropland vegetation progressed from annuals to a mixed short-grass, mid-grass, tall-grass community.

The effect of protection from grazing was somewhat different in a desert grassland of New Mexico (Gardner 1950). Here 30 years of protection resulted in a 110 % increase in grass density (the number of individuals per unit area), but there was little change in species composition. In another desert grassland in southern Arizona, shrub invasion on three plots was studied for 18 years (Brown 1950). One plot was protected from all mammalian herbivores, another was open, and a third was protected from cattle but open to rodents. Mesquite (Prosopis velutina) increased on all three plots, but the increase was much greater on the plot grazed by cattle.

Arnold (1950) used exclosures in pine-bunchgrass ranges of northern Arizona to examine vegetation changes induced by cattle. After 29 years the herbaceous component of the exclosure was dominated by tall-bunchgrass species with a few perennial weeds and annuals present. Outside the exclosure, however, tall-bunchgrass species were rare, while grasses resistant to grazing, perennial weeds, and annuals were abundant.

In a study of grazing effects on Ponderosa pine (Pinus ponderosa) forests and range, two plateaus in central Washington were compared (Rummell 1951). One plateau had never been grazed by livestock; the other had been grazed for 40 years. The vegetation of the ungrazed table consisted of open Ponderosa pine stands with an herbaceous cover of 35 % density. The grazed table, however, supported a dense stand of trees with thin stands of grasses. Here the herbaceous cover had a density of 14 %. The total number of species was lower on the grazed table, and several palatable forbs and shrubs were lacking. The ungrazed plateau had a very dense understory of herbaceous plants which inhibited reproduction of pines.

A similar comparative study was made by Larson and Whitman (1942) on three adjacent mesas in the South Dakota badlands. One mesa had never been grazed by cattle, a second was used intermittently, and a third had been lightly grazed for 40 years. The protected mesa had a mixed grass prairie type of vegetation dominated by western wheatgrass (Agropyron smithii) and dryland sedges (Carex spp.). The intermittently grazed mesa had the same dominant species as were found in the protected mesa but included a large number of forbs and woody plants. The continuously grazed mesa supported a short-grass type community dominated by blue grama grass (Bouteloua gracilis). Such studies as these

clearly demonstrate that cattle grazing may alter the natural vegetation of an area. A summary of the detrimental effects of cattle includes the replacement of native species by non-natives, the encroachment of woody plants in grasslands, soil impoverishment, and the alteration of vegetation structure.

Range Management Practices

Many of the detrimental effects of livestock grazing upon vegetation may be overcome in part by careful management of the range involved. Three important considerations in any range management system are density of stocking, distribution of grazing animals, and grazing season.

Improper grazing or overgrazing may result in some of the changes in vegetation previously described. Changes in species composition, appearance of unpalatable plants or woody species, soil changes, and erosion are indicators of improper livestock numbers on a range (Stoddart & Smith 1943). Moore and Biddiscombe (1966) maintained that only very careful management and control of the stocking rate could restore the natural grassland prairie of North America from the "continual deterioration" which had occurred since the mid-19th century.

Even when the number of cattle grazed on a range is not excessive, unequal distribution may result in range damage. Cattle may congregate in accessible areas of range, on level ground, or around water holes (Stoddart & Smith 1943). Other factors which influence range or pasture utilization are distance from trails, distance from shade, slope, and aspect (Arnold 1964). Some of these problems may be overcome by fencing, herding, or developing water sources.

Another important aspect of range management is the season of grazing. Grazing during the early portion of the growing season is most damaging to the range, as plants may be greatly weakened and their productivity decreased (Ellison 1960). Late winter grazing may have the same effect (Stoddart & Smith 1943). Various systems have been devised to make the best use of rangeland by decreasing damage and deterioration. Deferred grazing allows a range area to produce seeds and new plants to establish. Another grazing system involves the rotation of cattle from area to area throughout the growing season. The most commonly used system in the western United States is a combination deferred-rotation system (Sampson 1952).

Additional difficulties in management arise when the range is grazed by big game animals as well as livestock. In low numbers these animals may complement livestock, as big game animals often have food preferences differing from those of cattle. Elk (Cervus canadensis), however, compete directly with cattle, as they consume a high percentage of grasses and prefer many of the same species as cattle. Pronghorn antelope

(Antilocapra americana) also occur on western ranges but seldom compete with cattle because of their preference for forbs and woody plants. Deer, which are normally browsers, may also share range with cattle in North America. Vegetation damage may occur where both deer and cattle must depend on browse for the bulk of their diet (Humphrey 1962).

Regions with Native Mammalian Herbivores

Cattle often have a detrimental impact on vegetation and soils where they are introduced herbivores. The urus (Bos primigeni) is the probable progenitor of domestic cattle. Although the urus is now extinct, its original range was Europe, North Africa, and southwestern Asia (Tomich 1969).

Native herbivores may also have an adverse effect on the vegetation of an area. Numerous herbivore studies have been done in Africa, a continent where herbivores and vegetation have evolved together. As a result of this selective action nearly all of the woody plants of the African savannah have thorns, i.e. Acacia spp. (Walter 1971). Grasses of the African savannah are also adapted to grazing by herbivores. Many of these grasses are stoloniferous and capable of surviving close cropping by animals.

In one study of the effects of elephants (Loxodonta africana) on the vegetation of Murchison Falls National Park in Uganda, Buechner and Dawkins (1961) studied six sample forest areas by aerial photographs. They found that in five of the six samples, decrease in trees with crown diameters of over 9m averaged 52% between 1932 and 1956. This decrease in tree cover ranged as high as 95%. In this area an overpopulation of elephants was changing woodland to grassland by girdling trees. This damage to trees had the effect of opening the forests up to grass invasion, thus increasing the severity of frequent fires. The elephants were also effective in altering the species composition of small forests. Holoptelea grandis trees, a component of these forests, were not debarked and thus could gain dominance.

Laws (1970) reviewed a number of studies of habitat change due to elephants. In Budungo Forest, Uganda, elephants maintained a vegetation of secondary growth by preventing the formation of a closed canopy. In Lake Manyara National Park of Tanzania, the canopy cover of Acacia tortilis woodlands had been reduced 33% in nine years through the destructive action of elephants. The vegetation of Tsavo National Park in Kenya had previously been Commiphora-Acacia bush, but was being converted into grassland due to large numbers of elephants feeding in the area. Baobab (Adansonia digitala) trees in this park were being killed by elephants at a rate of 2% per year. In Ruaha National Park, elephants damaged up to 94% of the regeneration of the natural bush vegetation in localized areas. Larger Acacia and baobab trees were also debarked and often killed. Elephant

damage in these areas was pronounced because of the constant shrinking of the animals' range and subsequent overcrowding in game preserves.

The hippopotamus (Hippopotamus amphibius) is another herbivore which may alter the natural African vegetation. Lock (1972) reported that overgrazing by hippopotami in Uganda's Queen Elizabeth National Park resulted in the conversion of dominant species of a grassland from Sporobolus stapfianus to S. pyramidalis. When these herbivores were excluded, the grassland developed into a mosaic of short grasses and long grasses with bare patches uniformly distributed.

East Africa supports numerous other large herbivores. Petrides (1956) described the combined effect of native herbivores and livestock on a Themeda-Acacia savannah. Native herbivores in the area included wildebeest (Chonnochaetes spp.), hartebeest (Alcelaphus spp.), gazelle (Gazella spp.), impala (Aepyceros melampus), eland (Taurotragus spp.), giraffe (Giraffa camelopardalis), zebra (Equus burchelli), and waterbuck (Kobus spp.). The impact of each individual herbivore species was not considered. Overgrazing by these animals resulted in the invasion of grassland by young shrubs and the exposure of bare ground. By the end of the dry season, over 55% of the area had no grasses over 1 1/2 inches tall; even unpalatable grasses were closely grazed. This deterioration of vegetation reduced carrying capacity of the range, thus diminishing game numbers in the area.

Talbot and Talbot (1963) compared the biomass of native ungulates to the biomass of livestock that East African savannah could support. They found that the savannah could maintain a wild ungulate biomass of from 70,000 to 100,000 pounds per square mile. This was several times higher than the maximum cattle biomass of 21,300 to 32,000 pounds per square mile for East Africa. A study of food habits revealed that cattle, goats, and sheep preferred only a few grass species. The native ungulates, by contrast, had complementary diets. The various native animals often preferred different classes of food, and favored food species were unique for each ungulate. This situation allowed all available vegetation to be used efficiently to support the high biomass of native herbivores.

Large native herbivores interact with natural vegetation in Sri Lanka (Ceylon). Here, as in Africa, elephants may alter the woody vegetation, although Sri Lanka elephants (Elephas maximus) tend to be less destructive than their African counterparts. Mueller-Dombois (1972) found that crown distortion of woody vegetation in Ruhuna National Park due to elephants was particularly high among plants characteristic of the early stages of succession. Undergrowth species composition was altered, and species less palatable to elephants became dominant. Elephants also affected the regeneration of some upper canopy trees. The main influence of elephants on vegetation in the area studied was the perpetuation of non-climax woody vegetation.

North America is a continent with many native herbivore species. Their effects on vegetation, however, are often difficult to assess because of the large numbers of livestock grazed in the same areas. Deer, several species of which are found in North America, may alter the species composition of vegetation by concentrating on preferred plant species. These palatable species vary with the region; white cedar (chomaecyparis thyoides) and witchhopple (Viburnum alnifolium) are favorites in New York, while ash (Fraxinus sp.) and greenbriar (Smilax sp.) are preferred plants in areas of Texas. The effect of this preference may be to eliminate favored plant species under high deer densities (Klein 1970).

Elk, a native North American herbivore, may overgraze favored areas and trample undergrowth, but most problems with vegetation change are due to the combined grazing of elk and cattle or sheep (Humphrey 1962). The grazing impact of pronghorn antelope is likewise difficult to analyze in areas where their range overlaps with that of domestic livestock, especially sheep (Buechner 1950). Antelope may have had more influence on vegetation before the 1880's, when they outnumbered bison on the western plains (Humphrey 1962).

The effect of the bison (Bison bison) on the Great Plains of North America has been the subject of some controversy. The vegetation of the Great Plains in pre-European times is presumed to have been tall prairie grasses in the east and short-grasses to the west with a central area of mid-grasses or an intergradation of tall- and short-grasses. It is speculated that 50 million bison grazed these plains in the early 1880's. The most commonly held view is that later cattle introductions changed the natural tall- or mid-grass plains into short-grass plains (Clark 1956). Larson (1940), however, considered the short-grass plains to be the true climax of the biome. He believed that the bison had much the same effect as the introduced cattle and that the tall-grass association only appeared under protection from grazing.

Even though the natural vegetation of North America may support various indigenous herbivores without serious damage, introduced herbivores may be very detrimental. Cattle are probably the most important animals in this group. Additionally, several introduced herbivores that have become feral may be influential in altering vegetation in localized areas.

McKnight (1964) reviewed the history, effects, and present distribution of feral livestock in North America. Horses (Equus caballus), introduced in the 1500's, were one of the earliest introductions, and at one time several million feral horses were present on the Great Plains. Now less than 34,000 remain in grasslands and sagebrush (Artemisia spp.) scrub of the west. Their effect on vegetation consists of damaging regenerating conifer seedlings and overgrazing semi-arid ranges. These horses may also compete with native elk, deer, and mountain sheep.

Burros (Equus asinus), native to northeast Africa, were also introduced to North America in the 16th century and, like horses, became feral. These animals were widely distributed throughout the western states, mainly in rugged mountains and deserts. Burros may overgraze desert vegetation, leading to a decrease in plant cover and accelerated soil erosion.

A few feral cattle and feral sheep exist in western states, but have little impact on the environment due to their low numbers. Feral goats are widely distributed in 27 states and may be very destructive to both vegetation and soil in limited areas. The most common feral ungulate of North America is the pig, which is particularly numerous in the southeastern and southwestern states. Being omnivores, hogs may compete with many native animals. These feral animals are damaging to forest growth because they destroy tree seedlings, and their rooting habits make them a pest in pastures and croplands (McKnight 1964).

Herbivores which are introduced to an area and become feral may have a serious impact on natural vegetation even though the same vegetation may support native herbivores without real damage. Ellison (1960) was of the opinion that "...the exact composition of climax vegetation probably cannot be maintained by any intensity of grazing or selection of species other than those exerted by pristine wildlife." It therefore seems reasonable to assume that the impact of such feral animals on the vegetation of regions without native herbivores might be even more dramatic.

Regions with Few or no Large Native Herbivores

Oceanic islands are most prominent among the ecosystems which have evolved in the absence of large mammalian herbivores. Even continents have been isolated in the past, leading to the development of insular phenomena in their biota. For example, both Australia and South America were isolated for long periods of time in the past. The effects of this long-continued isolation were impoverishment and endemicity in the Australian fauna and few sharply separable faunal strata in South America (Simpson 1965).

The native fauna of Australia is dominated by marsupials which arrived on the isolated continent prior to the invasion of placental mammals such as rodents and bats. Subsequently, these marsupials filled the majority of the ecological niches in Australia (Simpson 1965). Thus kangaroos, wallabies, and other marsupials were the only large grazing animals in Australia until the advent of the Europeans. The indigenous vegetation of Australia is characterized by a lack of thorny species. For example, the native mulga (Acacia aneura) bears no thorns, although species of this genus in Africa and elsewhere are quite thorny (Walter 1971).

One of the major native herbivores of Australia is the grey kangaroo (Macropus major). These animals do not browse, and although they crop herbaceous plants and grasses closely, they do not uproot them or damage their roots. An average grey kangaroo (weighing 70 pounds) eats less than half as much as an average sheep (weighing 100 pounds). Kangaroos are non-selective grazers and have no preference for any particular plants. These habits help explain why kangaroo grazing is not damaging to the Australian vegetation, contrasting with the impact of introduced sheep and cattle (Breeden & Breeden 1966).

Grazing by introduced animals has resulted in many vegetation changes in parts of Australia. In temperate woodlands of southern Australia, sheep grazing has resulted in the replacement of tall warm season grasses by short cool season perennials and annuals. Specifically, the native kangaroo grass (Themeda australis) which was formerly the dominant over extensive areas, has been supplanted by less palatable perennial grasses and annuals, including many introduced species. In more arid regions of Australia, the outcome of livestock grazing has been the increase of shrubs such as Acacia (Moore & Biddiscombe 1966). In the northeast portion of southern Australia, overgrazing by livestock has cleared the area of the native saltbush (Atriplex vesicaria) (Walter 1971). However, Moore (1966) raised the possibility that the original dominant grasses of western Australia might return if burning was controlled and deferred grazing was practiced.

Like Australia, the continent of South America was isolated by sea barriers for 70 million years during the Tertiary Period (Simpson 1965). The first invasion of animals was composed of marsupials, ungulates, edentates, and later rodents, which island-hopped to South America during its period of isolation. Then during the Pliocene Epoch, a land bridge connected North and South America, and numerous other groups of animals moved into South America from the north. These new invaders included carnivores, guanacos, tapirs, deer, and peccaries (Tayassu spp.). Perhaps as a result of competition with the newcomers, many of the more ancient species of animals became extinct. However, the South American fauna today remains quite distinct from that of other continents (Bates 1964).

One interesting aspect of the South American fauna is the large number of unique rodent species. In fact, rodent genera outnumber all other flightless land mammals in South America (Darlington 1965). The herbivores (including rodent species) that presently exist in this continent are notable for their small size. The only really large herbivores of South America are the tapirs (Tapirus spp.), which may weigh as much as 400 pounds (Bates 1964). Such unique animals are among the insular phenomena exhibited by the continent of South America.

Certain regions of South America are oddly lacking in large herbivores. For instance, the pampas, an extensive grassland

area in Argentina, has had no large herds of native hoofed mammals for more than a million years. The camel-like guanaco (Lama guanacoe) and several rodents are the only native herbivores presently found there (Bates 1964). The present utilization of the pampas for cattle grazing began with European colonization of South America and has resulted in alteration of the natural vegetation of that region due to replacement of native plant species (Darwin 1839).

The most striking examples of ecosystems which lack large herbivores occur not on continents, but on oceanic islands. Insular biota tend to be vulnerable to distrubance by non-native organisms. Carlquist (1974) observed, "Insular autochthones that evolve in the absence of large herbivores do not have any resistance to them with few exceptions."

Wallace (1911) described the changes in vegetation due to feral goats on the island of St. Helena, located over one thousand miles from Africa. When discovered, this island was covered with dense forest vegetation and had no large native herbivores. Goats were introduced in 1513, and by the 19th century the forests were almost totally destroyed. Soil was eroded away, exposing rock. By the time Wallace visited St. Helena, it was practically barren.

Laysan Island, one of the Leeward Hawaiian Islands, is another oceanic island whose vegetation was dramatically altered by the introduction of an herbivore, in this case the rabbit (Oryctolagus cuniculus). When the rabbit was introduced in 1903, the plant cover of grasses and shrubs was approximately the same as at the time of the island's discovery. After 40 years of supporting rabbits, only 4 out of 26 indigenous plant species were still growing there. Rabbits were removed in 1923, and the vegetation began to recover. When visited in 1961, many of the original plant species were present, and the vegetation structure seemed to be similar to that previously described (Lamoureux 1963).

Turbott (1948) described the effects of feral goats on Great Island, just north of New Zealand, another Pacific island with no native mammalian herbivores. Maori inhabitants had cleared away much of the original plant cover, but after their departure in 1840, the native forest seemed to be regenerating. Later goats were introduced to the island and remained for 60 years. At the end of that time the feral goats were destroyed, and the vegetation was examined. What had previously been a mixed coastal forest was by this time a sub-climax forest of kanuka (Leptospermum ericoides), a species of plant avoided by goats. Few remnants of the original forest were left. Two years after the goat removal some of the native forest plants seemed to be regenerating, and formerly bare soil was being colonized by indigenous herbs (Baylis 1948).

New Zealand itself has been the site of numerous large herbivore introductions. The endemic plants of New Zealand have little resistance to heavy grazing or browsing, as these pressures were non-existent during the evolution of the New Zealand flora (Howard 1965). Thomson (1922) reported that wild cattle, present since the early days of European settlement, were still abundant in the back country. These animals were responsible for the destruction of several native species of shrubs and trees, as well as numerous types of undergrowth plants. Wodzicki (1950) reviewed the distribution and effect on vegetation of the more important introduced mammals of New Zealand. Of 53 mammal species liberated, at least 34 have become established. Goats, first liberated in New Zealand by Captain Cook, seriously alter vegetation. By debarking trees and shrubs and removing undergrowth, these animals have opened up forest regions and caused accelerated erosion. Cook also introduced the pig into New Zealand, and it soon became established. This animal disturbs the native ground cover of herbs, grasses, and ferns and may even uproot small trees.

Later in the 19th and 20th centuries, nine species of deer were introduced into New Zealand, and eight of these became established. The most widespread of these are European red deer, (Cervus elaphus) which are found mainly in native forests, mountain tops, scrub, or tussock grasslands. These deer tend to disturb the normal developmental sequence of the native forest. Favoring native woody plants as food, these animals browse on shrubs, small trees, and tree ferns, prevent plant regeneration, destroy undergrowth, and trample the forest floor (Wodzicki 1950). As a result of these actions, red deer are responsible for thinning and opening up forests, completely denuding some areas, accelerating soil erosion, compacting soil, and increasing water run-off. In accessible areas the sub-alpine scrub vegetation has been nearly eliminated by these animals. A more subtle effect of red deer is an alteration in the botanical composition of indigenous forests favoring less palatable or more browse-resistant species (Howard 1965). The other species of introduced deer, including axis deer (Axis axis), fallow deer (Dama dama), Sambar (Cervus unicolor), Virginia deer (Odocoileus virginianus), Wapiti (Cervus canadensis), and moose (Alces alces) are more locally distributed but have effects similar to the red deer in these limited areas.

A more specific description of the effects of introduced mammals on New Zealand vegetation is given by Moore and Cranwell (1934). Through the action of goats and pigs (and formerly wild cattle), a native rain forest has been and continues to be converted into a grassland dominated by Microlaena avenacea, an endemic grass. Before disturbance, this rain forest consisted of a closed canopy of tall trees, a middle layer of trees, shrubs and tree ferns, and a floor cover of mosses and filmy ferns. Microlaena occurred only as widely scattered individuals on the forest floor. The introduced mammals strip bark off trees, destroy undergrowth, trample soil and surface roots, and prevent

seedling establishment. In this way the trees, shrubs, and even tree ferns finally disappear through direct destruction by animals, soil impoverishment, and increased wind at ground level. Microlaena, which is basically unpalatable, then becomes the complete dominant of the ground cover, and few other plants survive where once a rain forest stood.

Large Herbivores in the Hawaiian Islands

The Hawaiian Islands are still another example of an oceanic island ecosystem which evolved in the absence of large mammalian herbivores. In fact, the only mammals indigenous to these islands are the monk seal and one species of bat (Tomich 1969). In addition to these, Hawaiians introduced the pig, the dog (Canis familiaris), and the Polynesian rat (Rathus exulans). It was not until the 18th century that herbivores such as cattle, sheep and goats were introduced by European explorers. Referring to the Hawaiian Islands, Carlquist (1974) wrote that it was "...impossible to imagine evolution of the present species composition and growth forms and these herbivores been present as early, prehuman immigrants."

The Hawaiian flora is characteristically lacking in mechanisms to deter herbivores. Very few native Hawaiian plants are known to be poisonous. Exceptions are Cocculus ferrandianus and possibly Wikstroemia oahuensis (Carlquist 1970). Two other native plants may be considered potentially poisonous. Erythrina sandwicensis, the endemic wiliwili tree, contains small quantities of alkaloids in its seeds, and the Hawaiian prickly poppy (Argemone glauca) has potentially poisonous chemical properties as well as prickles (Arnold 1971). Strongly scented oils that may discourage herbivores are for the most part absent from the indigenous flora. Structural deterrents such as spines and throns are likewise rarely present. For example, the Hawaiian raspberry (Rubus hawaiiensis) is often thornless (Carlquist 1970).

The goat was first introduced to the island of Ni'ihau by Captain James Cook in 1778. A few years later, Captain George Vancouver landed more of these animals on Kaua'i, Hawai'i, and Maui. Goats were later released on the other major Hawaiian Islands, where their descendents still exist today (Kramer 1971).

The effect of feral goats on the vegetation of Haleakala National Park has been described by Yocum (1967). He estimated that 600 goats lived in the crater at that time, a decrease from the thousands that existed in the area during the previous decade. Overgrazing by goats on native vegetation has resulted in the dominance of the native pukiawe (Styphelia tameiameiae) in some communities, the opening of other native stands, and the spread of introduced annuals. Goats have also been a factor in increased soil erosion due to elimination of plant cover, disturbance of soil, and promotion of landslides.

Another study of the effects of feral goats on vegetation was carried out by Mueller-Dombois and Spatz (1975) using three exclosures in the coastal lowlands of Hawaii Volcanoes National Park. One exclosure was located in an annual grassland, and the other two were placed in a perennial grassland area on deep ash soil. After two years of goat exclusion, both qualitative and quantitative changes were noted in the annual grassland exclosure. Five perennial bunchgrass species occurred inside the exclosure, but were absent on the outside. The dominant plant inside the exclosure was Canavalia kauensis, an endemic vine which was present outside only as a few seedlings during the wet season. The two exclosures in the perennial grassland did not exhibit such striking changes during a year's study. In one of these exclosures, several grasses, a forb, and two shrubs had greater increases in cover inside than outside the exclosure. The second exclosure in this area also had similar vegetation cover within and without, although one grass species and several shrubs (particularly seedlings) did increase inside. This study indicated that the vegetation of this coastal lowland area might be quite different in the absence of grazing pressure from goats, and that recovery of some native species in the area might be feasible.

Sheep were introduced into the Hawaiian Islands soon after their discovery by Europeans. Vancouver brought along domestic sheep on both his second and third voyages to Hawai'i. A kapu was placed on the sheep, and they soon multiplied. By 1851 there were thousands of feral sheep on Hawai'i, Maui, Moloka'i, and Kaua'i (Kramer 1971). Sheep were raised on Kaho'olawe and Lana'i in the past, and some domestic sheep were still being ranched on Ni'ihau and Parker Ranch of the Big Island in the 1960's (Tomich 1969). The peak of sheep production was in 1884, when over 121,000 domestic sheep were found in the Hawaiian Islands (Henke 1929).

The largest concentration of feral sheep in the islands is present on Mauna Kea of the island of Hawai'i. In 1937 the Mauna Kea sheep population was estimated at 40,000, and between the years of 1921 and 1945, over 70,000 were killed in this area (Tomich 1969). The present sheep population on Mauna Kea is much lower than in previous times, due in part to a recent court-ordered eradication attempt by the State Division of Forestry and Wildlife. These sheep have a great impact on the mamane (Sophora chrysophylla) forests indigenous to the mountain. Overgrazing causes death of existing trees, prevents mamane regeneration, and greatly decreases ground cover (Kramer 1971). According to Warner (1960), feral sheep are responsible for the loss of 90% of the top soil and 40% of the mamane trees in this formerly forested region.

Another species of sheep, the mouflon (Ovis musimon), has been recently introduced, first on Lana'i in 1954 and then on Mauna Kea of Hawai'i in 1963. The purpose of the latter liberation was the hybridization of these mouflon sheep with the

feral sheep already present. Mouflon tend to be less destructive to vegetation, mainly because of their tendency to congregate in small bands rather than large herds (Tomich 1969).

The earliest introduced large herbivore was the pig, which the Polynesians brought to Hawai'i. These pigs, of Asian ancestry, were small and apparently remained in domestication (Tomich 1969). These animals were abundant before the European discovery of Hawai'i, but were eventually absorbed into the pig stock introduced by Cook and later Europeans. Wild pigs are presently found on all the main Hawaiian Islands except Lana'i and Kaho'olawe, but the island of Hawai'i has the largest and densest population (Kramer 1971). The major impact of feral pigs on vegetation occurs in upland forests, although they also eat grasses and root in ranch pastures. In rain forests pigs disturb the forest floor and root up or feed on native plants such as Acacia koa seedlings (Cooray 1974).

More recent mammal introductions include axis deer (Axis axis), blacktail deer (Odocoileus hemionus), and pronghorn antelope (Antilocapra americana). Axis deer were first brought to the islands as a gift to Kamehameha V. They were released in 1868 on Moloka'i, where they increased to a population of about 7000 by 1900 (Kramer 1971). A small number of these deer also existed on O'ahu in Moanalua Valley and around Diamond Head. In 1920 axis deer were also liberated on Lana'i where they became established and remain today. Also present on the island of Lana'i is a herd of several hundred pronghorn antelope, which were introduced from Montana in 1959. Examination of stomach contents indicates that exotic plants such as haole koa (Leucaena leucocephala), Lantana camara, Bidens sp., Emilia sp., pineapple (Ananas comosus), and red top grass (Rhynchelytrum repens) are the most important constituents of the pronghorn diet (Kramer 1971).

Even more recently in 1961, Columbian blacktail deer (or mule deer) were imported from Oregon and introduced to Kaua'i by the Hawaii Division of Fish and Game. As of 1972, an estimated 575 deer existed in the Puu Ka Pele and Kekaha game management areas (Telfer 1973). Analysis of rumen samples has revealed that at least 37 plant species are taken as food by the deer. The chief food plant seems to be guava (Psidium guayava), but at least seven native plants are also eaten. Among these is Acacia koa which apparently constitutes a considerable part of the deer diet (Telfer 1971). Plant density and coverage measurements from a deer exclosure in the area indicate that browsing reduces the number of Acacia koa seedlings as well as the koa canopy cover. The cover of liliko`i (Passiflora edulis) and the indigenous `uki`uki (Dianella sp.) were also decreased (Telfer 1972). The deer may also alter vegetation by trampling underbrush, opening up the forest, and creating deer trails (Telfer 1971).

The introduced herbivore that has probably had the most profound effect on Hawaiian vegetation is cattle. This animal

was brought to Hawai'i by Captain George Vancouver on his second voyage in 1793 and also on his third voyage in 1794. A kapu or prohibition against killing the animals was enforced, and they multiplied quickly. Feral cattle became abundant on Kaua'i, O'ahu, Moloka'i Maui, and Hawai'i (Tomich 1969). According to the missionary Ellis (1917), there were "immense herds" of wild cattle on Mauna Kea of Hawai'i in 1823. Bloxam, who visited O'ahu in 1825, noted that many cattle, goats, and horses were present on that island. In fact, around 1850 many wild and domestic cattle were roaming about in the vicinity of Honolulu (Kramer 1971). By the end of the 19th century feral cattle were being heavily hunted, and now relatively few truly feral cattle remain in the Hawaiian Islands.

One remaining herd is found in the Honaunau Forest Reserve of the island of Hawai'i, where large numbers of feral cattle have roamed in the past. In 1956 at least 1000 feral cattle existed in the area, but this number was reduced when 600 head were shot during 1958 (Carlson and Bryan 1959). These feral cattle seemed to be interfering with the reproduction of such native plant species as koa and sandalwood (Santalum spp.). Judd (1927) considered cattle, feral or domestic, to be the most important factor in the destruction of Hawaiian forests. By disturbing undergrowth cattle prevent the natural increase of trees, change the moisture and wind conditions of the forest floor, and open up the forest to "rank" grasses, such as Hilo grass (Paspalum conjugatum).

In 1851 an estimated 12,000 feral cattle roamed the island of Hawai'i, far outnumbering the domestic cattle of that island The number of domestic cattle increased steadily from then, and by 1927, approximately 158,000 cattle were being raised on more than a million acres of ranchland in Hawai'i (Henke 1929). However, the effect of domestic cattle on unmanaged natural vegetation is much the same as that of feral cattle. According to Egler (1947), cattle were partly responsible for conversion of the woody vegetation of southeast O'ahu into grasslands, which include many exotic grasses. Erosion occurred and the grasslands were ineffective in holding new soil. Other areas of O'ahu altered by cattle grazing include Manoa Valley where the natural forest cover has been replaced by guava, lantana, and other exotic weeds (Campbell 1920).

Skottsberg (1953) described the destruction of a native dry forest on northwest Lana'i due to cattle grazing. Native sandalwood trees were dying, and no sandalwood seedlings or any other native plants were present in the ground cover. Campbell (1920) reported the complete destruction by cattle of much of the forest on the drier slopes of Haleakala on Maui.

Much of the vegetation of the island of Hawai'i has been affected by cattle grazing. After 30 years of grazing, much of the native dry forest near Pu`uwa`awa`a had been destroyed, and the area was opened up to exotic plants such as Opuntia

megacantha cactus and koa haole (Leucaena leucocephala) (Hatheway 1952). Endemic plants remaining in this dry forest, such as Kokia drynarioides and Hibiscadelphus hualalaiensis, were no longer reproducing (Skottsberg 1953). In the Kohala mountain district of Hawai'i native koaia (Acacia koaia) forests have almost disappeared as a result of grazing. The plains of the Waimea area of Hawai'i were once heavily forested, but have been deforested mainly through the agency of cattle (Anonymous 1856, cited by Baldwin & Fagerlund 1943).

Likewise, many changes have occurred in the vegetation of the Kilauea Volcano region of Hawai'i. Campbell (1920) described the area along the Volcano road as an "unspoiled rain forest" in 1892. On a return visit in 1919, he reported that little of the rain forest was left due to cutting and disturbance by cattle grazing.

The Mountain Parkland Ecosystem of Hawaii

Just as other areas of the island of Hawai'i have been changed, the mountain parkland region has been greatly influenced by introduced herbivores in the past. A mountain parkland belt is found on the eastern slope of Mauna Loa between the elevations of 4500 feet (1372 m) and 6600 feet (2012 m). A portion of the Mauna Loa strip of the Hawaii Volcanoes National Park, as well as sections of the adjacent ranches, may be included in this mountain parkland belt. This type of vegetation was previously present also on the moist slopes of Mauna Kea and Hualalai (Robyns & Lamb 1939). The parkland ecosystem on Mauna Kea is no longer intact, as the area is used for cattle ranching. Tree regeneration is prevented, and native grasses are less important than introduced species (Mueller-Dombois & Krajina 1968).

A parkland formation is not a uniform vegetation type, but rather a "macro-mosaic" containing many different communities (Walter 1971). In the Mauna Loa parkland, at least three main types of communities may be recognized: grass communities, shrub communities, and tree communities (mostly Acacia koa) (Mueller-Dombois 1967). Using a synthesis table technique, Newell (1968) included the mountain parkland in an Acacia koa-Holcus lanatus alliance, and specified two character (actually differential) species for the area: Panicum tenuifolium, a native grass, and sheep sorrel (Rumex acetosella), an introduced herb.

The mountain parkland appears as a distinct band along the east flank of Mauna Loa, and is bounded at its lower limit by an Acacia koa-Sapindus saponaria savanna where the rainfall is higher and the soil is deeper. The formation above the parkland consists of a Metrosideros scrub-forest and includes some Sophora chrysophylla trees, which are also present in the parkland ecosystem (Mueller-Dombois 1967).

The mountain parkland is a dynamic ecosystem with the cover of the various communities subject to change (Mueller-Dombois 1967). Despite this fact and the influence of human and introduced herbivore activity in the region, it seems that the present vegetation of the parkland within the Hawaii Volcanoes National Park is similar to that of pre-European times. Archibald Menzies, the first European to reach the summit of Mauna Loa, passed through the parkland region in 1794. Ascending the southeast slope above Kapapala, he described the vegetation halfway up the wooded portion of the mountain as clumps or groves of trees and grassy spots (Menzies 1920). On a later ascent of Mauna Loa in 1834, the botanist David Douglas described grassy plains with mamane trees above koa forests and below "brushwood" (Wilson 1919). Fosberg (1972) referred to the grasslands of the ash slopes of the island of Hawai'i as "tussock grasslands." This category would include grassland communities in the mountain parkland. Because of the number of endemic grass species in these grasslands, Fosberg believed that they had been part of the natural vegetation of the Hawaiian mountains for a long time.

Vogl (1969) is of the opinion that the mountain parkland is, at least in part, maintained by fire. Fire may retard the spread of Acacia koa trees into the grassland matrix, but apart from this factor, the native bunchgrass communities of the ecosystem are not dependent upon fire. These parkland grasslands have apparently "...survived repeated, widespread, and severe fires" in the past. Vogl cites as an example a fire on the slopes of Mauna Loa in 1924 which burned 12 square miles of open forest between elevations of 5600 and 7200 feet. Mueller-Dombois and Lamoureux (1967) studied the soils of Kipuka Ki and Kipuka Puaulu, just below the Mauna Loa mountain parkland. Soil pits revealed fragments of charcoal in the forest soils of these kipukas which were dated at 2000 years old, indicating that fire had occurred during their development. Analysis of the savannah soils of the two kipukas implied that the grass-dominated savannah vegetation may have originated after a fire.

Other disturbance factors include introduced herbivores such as goats, pigs, and cattle. Much of the mountain parkland outside the Park has been overgrazed by both feral and domestic animals so that the original vegetation cover is gone. In particular, grasses have invaded former forest areas (Robyns & Lamb 1939).

Effects of Feral Herbivores on Parkland Vegetation

One of the major effects of feral goats on the vegetation of the mountain parkland is interference with the vegetative reproduction of Acacia koa. Spatz and Mueller-Dombois (1973) used an exclosure near the Mauna Loa Strip Road of the Hawaii Volcanoes National Park to analyze the goat damage in koa colonies. After three years of protection, koa root suckers were counted, measured, and mapped along ten transects run through the

exclosure. These data were compared with that collected from transects of six other unfenced koa colonies. Results showed that koa suckers below 10 cm in height were numerous in the areas browsed by goats, but larger koa suckers were rare and exhibited signs of goat damage. In contrast, many koa suckers above 10 cm in height were present within the exclosure, with size classes from 10 cm to 1 m being well represented. These results indicate that a large population of goats in localized areas of the mountain parkland may seriously hamper the reproduction of Acacia koa and thus alter the structure of the ecosystem.

The feral pig is also found in the mountain parkland ecosystem of Mauna Loa. Spatz and Mueller-Dombois (1975) studied the patterns of plant succession after pig disturbance in the grasslands of the ecosystem. Several plots were established in a frequently pig-disturbed area in the upper part of the parkland (1880 m or 6200 ft elevation). Prior to the beginning of the study, the native grasses such as Deschampsia australis and Panicum tenuifolium had been uprooted and strewn about by pigs. These endemic grasses and the indigenous sedge Carex macloviana were still present at the edges of the plot. Nevertheless, during the following year the introduced velvet grass (Holcus lanatus) invaded the disturbed plot and became the dominant species. At the same site, transects were laid out over areas with different degrees of pig disturbance. An examination of the plant succession along these transects indicated that the endemic grasses, Deschampsia and Panicum, could reoccupy areas that were not continuously disturbed.

Results from artificially disturbed plots at another parkland site suggest that the disturbance of digging and leaving the uprooted plants favors succession of introduced plants. By contrast, artificially scalped and cleared plots were invaded by the endemic Deschampsia australis as well as the introduced Holcus lanatus. These findings demonstrate that continued pig disturbance could drastically influence the species composition of the Mauna Loa grasslands, through replacement of native species by exotic grasses.

Cattle Grazing in the Mauna Loa Mountain Parkland

Most of the mountian parkland ecosystem has been much changed through grazing of introduced herbivores. Feral goats and pigs have been and remain a factor influencing the vegetation, but the most important mammalian herbivores in the parkland as a whole are domestic cattle. Much of the Mauna Loa parkland ecosystem has been converted into cattle ranches, although a portion remains within the Mauna Loa strip of the Hawaii Volcanoes National Park.

Cattle have grazed in the mountain parkland for well over 100 years (Fagerlund 1943). This grazing continued even after the inclusion of the Mauna Loa strip into the National Park. The

history of cattle grazing in the Hawaii Volcanoes National Park has been reviewed by Apple (1954). The National Park was established in 1916, but the Mauna Loa strip (encompassing 46,050 acres) was not added until 1927. The mountain parkland portion of the strip addition had been considered choice grazing land, so the Territorial government reserved grazing rights in the strip and leased them to Kapapala Ranch. This situation continued unchallenged until the 1930's when two foresters, C. S. Judd and L. W. Bryan, complained that Acacia koa in the area was not reproducing. As a result, the Park Superintendent asked the Territorial governor to suspend grazing on the Mauna Loa strip, but no action was taken.

Then in 1936, the adjacent ranch which had leased grazing rights in the park decided to clear shrubs and thickets (mostly Styphelia and Dodonaea) on park land to facilitate cattle round-up. The Park Superintendent objected and the clearing action ceased. This episode was the beginning of a controversy between the Territory of Hawaii and the National Park over control of the Mauna Loa strip. The difference was settled in 1938 when the Secretary of the Interior instructed the Director of the National Park Service to terminate grazing within the Park, because the Territory's claim to grazing rights in the area was void.

By 1940 all cattle had been removed from the Mauna Loa strip sector of the National Park. However, this release from cattle grazing lasted only 18 months. After the Second World War broke out, Kapapala Ranch, which had formerly leased grazing rights to the strip, requested that their lease be renewed. The Park Superintendent denied the request, but was ordered by the military governor to permit grazing within the National Park. Therefore, cattle grazing returned to the mountain parkland portion of the National Park in 1942 and continued until 1948. At that time over 300 cattle were removed from the Mauna Loa strip, and the ban on grazing has continued to the present.

Although the detrimental effects of cattle grazing on Hawaiian vegetation in general have been recognized for some time, few quantitative analyses of cattle damage in the Mauna Loa mountain parkland have been attempted. One such study by Baldwin and Fagerlund (1943) compared the number and size of Acacia koa trees in three pairs of plots in the National Park. One plot pair had been free of cattle grazing for six years; another pair of plots was ungrazed for six months; and the third plot pair was continuously grazed. In the six year old exclosures, a large number of koa saplings approximately 12 feet in height were counted. The six month old exclosures had an abundance of young root suckers, up to 30 inches in height, but older saplings were absent. The continuously grazed pair of plots had no saplings and few suckers. Those root suckers that were present were under six inches in height and had been browsed and trampled. The conclusion of the authors was that cattle grazing suppressed koa reproduction and prevented the perpetuation of the natural koa

groves. These findings were supported by analysis of aerial photographs of the Mauna Loa strip of the Hawaii Volcanoes National Park after cattle had been removed. Comparison of two sets of these photographs, taken 11 years apart, showed that koa colonies were penetrating the grasslands through expansion from root-suckering at a rate of 0.5-2.5 m per year (Mueller-Dombois & Krajina 1968).

Although cattle have been eliminated from the National Park, grazing continues on the two ranches adjacent to the Mauna Loa strip. Vestiges of the former parkland vegetation remain in the introduced grass communities of these ranches. Decadent and dead Acacia koa and Sophora chrysophylla trees, Styphelia and Vaccinium shrubs, and patches of native grasses in protected spots are indicators of the former vegetation cover on Keauhou Ranch.

The present grassland communities of Keauhou Ranch were classified and mapped by Spatz (1973). Analysis of yields of dry matter and protein in the various pasture communities revealed that only a small portion of the ranch was actually productive pasture. Spatz recommended that half of the ranchland now grazed be retained as pasture and improved. The rest of the ranch pastures could then be devoted to alternative uses such as cultivated koa forest, thereby increasing the efficiency of land use. It is difficult to imagine the natural parkland vegetation reappearing independently in an area so altered by grazing, even though the seed source for native plants is present in the National Park. However, a recovery of downgraded native vegetation in the absence of herbivores is not inconceivable.

INTRODUCTION

As is the case with most other oceanic islands, the Hawaiian Islands have virtually no indigenous mammals. Previous to the arrival of humans, these islands supported only two such species. The Polynesians who first peopled the Hawaiian Islands brought three species of mammals with them: the dog, the pig, and the Polynesian rat. It was only with the advent of Europeans in the late 18th century that Hawai'i began to be populated with large herbivores having the potential to greatly alter the vegetation.

The effects of introduced herbivores on the flora of the Hawaiian Islands have been devastating. As the plant species of the Hawaiian Islands have evolved in the absence of any grazing pressure, they are largely lacking in mechanisms to deter large herbivores (Carlquist 1970).

The mountain parkland ecosystem, with its history of cattle grazing, provides an opportunity to closely examine the consequences of this grazing in a natural Hawaiian vegetation type. By comparing two portions of the same ecosystem separated for 30 years into a grazed ranch area and a segment protected by inclusion into the Hawaii Volcanoes National Park, the impact of cattle on this ecosystem may be detailed. The objective of this study is to determine the effects that cattle have had on the vegetation and soils of the mountain parkland.

Three hypotheses are presented here: the first, that cattle grazing has altered the structure and floristic composition of the parkland ecosystem; the second, that cattle grazing has suppressed altitudinal variation in plant communities of the ecosystem; and thirdly, that soil physical and chemical properties have been impaired under the influence of cattle grazing. Thus the objectives of this study were to compare the vegetation structure, floristic composition, and soil properties of the ungrazed area in the National Park and the grazed area in the adjacent Keauhou Ranch, and to examine them for differences which might be attributed to cattle grazing. Despite the presence of other introduced mammals in the mountain parkland, cattle grazing has been the major factor in the alteration of the vegetation of the parkland ecosystem. Continued cattle grazing on the portion of the parkland within Keauhou Ranch has resulted in the conversion of grasslands dominated by native plants into pastures of introduced grass species, even though the seed of native grasses is available in the adjacent park.

THE STUDY AREA

Geography, Geology, and Soils

The area studied is the mountain parkland ecosystem on the east flank of Mauna Loa of Hawai'i, the largest of the Hawaiian Islands. This ecosystem was first designated "mountain parkland" by Robyns and Lamb (1939). The mountain parkland is found between 4500 feet (1372 m) and 6600 feet (2012 m) elevation on Mauna Loa, a mountain whose summit is 13,680 feet (4170 m) above sea level. Study sites are located in the Mauna Loa strip portion of the Hawaii Volcanoes National Park and in Keauhou Ranch adjacent to the park (Fig. 1).

The substrate of the mountain parkland consists of prehistoric lava flows of the Ka`u (and possibly Kahuku) volcanic Series which covers a major part of the mountain. Both 'a'a and pahoehoe lavas are present and individual flows average 15 feet in thickness (Macdonald & Abbott 1970). The Keamoku lava flows, late prehistoric 'a'a flows which are found on Keauhou Ranch and down the center of the Mauna Loa strip, are more recent than most of the flows in the mountain parkland (Peterson 1967). These lavas appear to be recent but cannot be attributed to any historic flow, thus the term late prehistoric.

The lower lavas of Mauna Loa are covered by variable ash deposits. In the mountain parkland ecosystem these ash deposits are shallow and discontinuous with occasional rock outcroppings. Two types of ash are present: light brown Pahala ash and more recent grayish ash of Kilauea or Halemaumau origin. The average depth of soil is 20 to 25 cm (Doty & Mueller-Dombois 1966). The ash soils of the mountain parkland may be classified as andept Inceptisols in the modern system of soil taxonomy (Sato et al. 1973). These soils were previously classified as intrazonal soils of the Brown Forest Soil Great Soil Group (Cline et al. 1955).

Mountain parkland soils of the study sites may be placed into the Hanipoe and Apakuie Soil Series. Parkland soils of the Hanipoe Series are either silty loam or stony loam of 12 to 20% slope. These soils are moderately well developed with an A and a B horizon. A notable characteristic of this soil series is a distinct red band in the lower portion of the A horizon. Apakuie Series soils of the area are very stony, very fine sandy loam with a 12 to 20% slope. The upper reaches of the mountain parkland have a high proportion of area mapped as rockland or very stony land (Sato et al. 1973).

Climate

The mountain parkland ecosystem has a summer-dry climate with a mean annual rainfall of 1250 mm (Mueller-Dombois 1967).

Two International Biological Program (IBP) weather stations are present in the parkland along the Mauna Loa strip road: one at 5400 feet (1645 m) elevation and another at 6600 feet (2012 m), which is the upper limit of the ecosystem.

Rainfall and temperature data from these stations were displayed in climate diagrams (Bridges & Carey 1973, 1974, 1975), which exhibit the summer-dry aspect of the parkland climate. These climate data of 1972, 1973 and 1974 detail weather conditions concomitant with the period during which field sampling was undertaken for the present study of parkland vegetation. In 1972, the climatic diagram for the station at 5400 feet elevation shows dry periods occurring in the months of May and July, separated by a wetter June. The 1973 diagram for this station exhibits a pronounced dry period from May through August and an additional one in January. In 1974, the arid interval was again from May to August. The climate diagrams for the station at 5400 feet elevation indicated some variation in the wettest months for the three years. In 1972, months with more than 100 mm rainfall were January, February, March, April, November, and December. The wettest months of 1973 were March, October, and November. In 1974, March, April, November, and December had more than 100 mm precipitation. Total rainfall at this station was approximately 900 mm in 1973 and 1200 mm in 1974. Interception of fog may make a substantial contribution to precipitation in the portion of the parkland above 4920 feet (1500 meters) elevation. This fog and cloud water interception may be particularly important during the dry summer months (Juvik & Perreira 1973).

Data from the weather station at 6600 feet elevation produced climate diagrams similar to those for the lower station. The dry period for all three years occurred during June and July, but it was less severe than the one at 5400 feet elevation. An additional dry interval occurred in January of 1973, paralleling a January drought at 5400 feet elevation. As with the lower station, there was some variation in months with the most rainfall. In 1972, January, April, November, and December were the wettest months. Months with the highest rainfall in 1973 were February, September, October, and November. In 1974, March, April, November, and December were months with more than 100 mm precipitation. Cumulative rainfall for this upper parkland station was approximately 1650 mm in 1973 and 1350 mm in 1974.

Mean annual temperatures for the two parkland stations differed, with the upper site being somewhat colder. The mean annual temperature for the 5400 feet elevation station was 13.08°C in 1972, 13.33°C in 1973, and 12.67°C in 1974. At the 6600 feet elevation station mean annual temperatures for the three years of 1972, 1973, and 1974 were 10.67°C, 10.50°C, and 10.42°C, respectively. At the lower station monthly maximum temperatures ranged from 19°C to 30°C, and monthly minimum temperatures ranged from 0°C to 11°C for the years 1972-74. Monthly maximum temperatures of 13°C to 25°C and monthly minimum

temperatures of -6°C to 6°C were recorded at the upper site (Bridges & Carey 1973, 1974, 1975).

Frost does not seem to be an important element in the climate at the 5400 feet elevation. In 1973, no temperatures below 0°C (32°F) were recorded, and in 1974, only one day (in September) had a recorded minimum temperature of 0°C or below. Naturally, temperatures are lower at 6600 feet elevation, and frost occurs more frequently. During 1973, six days had recorded temperature of 0°C or below. These low temperatures occurred in February; all other months were apparently frost-free. During 1974, 33 days had minimum temperatures at or below the freezing point. These days with potential frost were distributed throughout the first four months of the year as follows: January, six days; February, 22 days; March, four days; and April, one day (Bridges & Carey 1974, 1975).

Month to month mean relative humidity for the weather station at 5400 feet elevation ranged between 61 and 93% saturation over the years of 1972, 1973, and 1974. Month to month minimum relative humidity varied from 9 to 84% while the month to month maximum relative humidity was always 100% during the same three years. The mean annual relative humidity was 77% in 1973 and 82% in 1974. At the upper station month to month mean relative humidity values were between 50 and 88%; month to month minimum relative humidity ranged between 8 and 32%; and monthly maximums were all 100% during the years 1972-74. Mean relative humidity at 6600 feet elevation was 69% for 1973 and 77% for 1974 (Bridges & Carey 1973, 1974, 1975).

Vegetation

A parkland formation is a non-uniform vegetation type or "macro-mosaic" containing different plant communities (Walter 1971). The three basic communities of the Mauna Loa mountain parkland are grass communities, shrub communities, and tree communities (Mueller-Dombois 1967). The grass communities contain both native and exotic grass and herb species, while the shrub communities are basically composed of native shrubs. The dominant tree in the parkland is Acacia koa (koa), but Sophora chrysophylla (mamane) and Metrosideros polymorpha (ʻohiʻa-lehua) are also present.

Using a synthesis table technique, Newell (1968) included the mountain parkland in an Acacia koa-Holcus lanatus (velvetgrass) alliance, and specified two character (actually differential) species for the area: Panicum tenuifolium, a native grass, and Rumex acetosella (sheep sorrel), an introduced herb. Several different schemes for vegetation zonation have placed the mountain parkland in various zones. Hillebrand (1888) called the zone in which the mountain parkland occurs the upper forest-zone. Rock (1913) and others also referred to this zone as the upper forest region. Robyns and Lamb (1939) placed the

mountain parkland in a specific Parkland zone. In the plan of Hartt and Neal (1940), who worked on Mauna Kea, the mountain parkland would be placed into the subalpine zone. The mountain parkland ecosystem was included in the E(1) zone of Ripperton and Hosaka (1942). The natural cover of this zone was described as open forest and shrub used for dry range. Krajina (1963) utilized the scheme of Ripperton and Hosaka for his biogeoclimatic zones which are based on climate and soils as well as vegetation cover. The mountain parkland falls in the subhumid mesothermal zonal group of Krajina where vegetation cover is described as mixed mesophytic and xerophytic, more or less open scrub forest. Mueller-Dombois (1976) incorporated the mountain parkland into a montane seasonal zone extending from 3800 to 6700 feet elevation on Mauna Loa.

The present vegetation of the mountain parkland ecosystem within the Hawaii Volcanoes National Park is apparently similar to that of pre-European times. Archibald Menzies, the first European to reach the summit of Mauna Loa, passed through the parkland region in 1794 and described the vegetation halfway up the wooded portion of Mauna Loa as clumps or groves of trees and grassy spots (Menzies 1920). In 1834, the botanist David Douglas described a portion of the slopes of Mauna Loa as grassy plains with mamane trees above koa forests and below "brushwood" (Wilson 1919).

Fires have occurred in the past in the mountain parkland (Mueller-Dombois 1967; Vogl 1969) and in the kipukas and savanna below the parkland ecosystem (Mueller-Dombois & Lamoureux 1967). Fires started by lava flows may have encouraged the expansion of the grasslands of the parkland ecosystem (Mueller-Dombois 1967). Fire may retard the spread of koa trees into the grassland matrix, but according to Vogl (1969), the native bunchgrass communities of the ecosystem are "possibly not dependent on fire, except in forest-shrub ecotones..."

Disturbance by introduced herbivores has been an important factor in the alteration of vegetation in the mountain parkland. Feral goats, descended from European introductions in the 18th and 19th centuries (Kramer 1971), are present in the ecosystem. These animals may alter the structure of the parkland ecosystem by interfering with the reproduction of koa trees (Spatz and Mueller-Dombois 1973). The feral pig, a Polynesian and early European introduction, is another herbivore found in the area. A study of plant succession after pig disturbance (Spatz & Mueller-Dombois 1975) indicated that continuous pig digging may result in replacement of native grasses by exotic species. Another important mammalian species introduced into the parkland is cattle which have grazed in the mountain parkland for over 100 years (Fagerlund 1947). Even though the Mauna Loa strip was added to Hawaii Volcanoes National Park in 1927, cattle grazing continued within the park until 1948. In a study of the effects of cattle on the woody vegetation of the mountain parkland carried out before the cessation of grazing. Baldwin and

Fagerlund (1943) concluded that browsing and trampling by cattle prevented natural koa reproduction. Although cattle are no longer permitted within the National Park, cattle grazing continues in the adjacent ranches. This situation permits a comparative study of the two areas, for the purpose of determining the effects of cattle on the vegetation of the ecosystem.

METHODS

Field Procedure

Site selection.--After reconnaisance, 16 sites were chosen along the Mauna Loa Strip Road. Sampling sites were placed systematically along the Hawaii Volcanoes National Park-Keauhou Ranch boundary within the mountain parkland ecosystem. Unless the distribution of plants is random, such a sampling plan may best represent the vegetation of an area as large as the mountain parkland. The fenced boundary line between park and ranch separates two portions of the same ecosystem and effectively serves to exclude cattle from the part of the parkland included in the National Park.

Beginning at 4600 feet elevation, paired sites were placed at intervals of 200 feet in altitude up to an elevation of 6000 feet. A pair of sites was established at each chosen elevation, one within the Hawaii Volcanoes National Park and one inside the Keauhou Ranch. Except for the two uppermost elevations, the two sites in a pair were quite close to one another. In some cases, paired sites were directly across the boundary fence from each other. Due to a lava flow which ran along the park-ranch boundary above 5400 feet elevation, the two upper ranch sites were placed further into the ranch, east of the park boundary.

Vegetation sampling.--Relevē placement was restricted to relatively level areas away from such obvious disturbances as roads, jeep trails, and cattle paths. Depressions and rocky outcroppings were avoided. When possible, relevēs were located within sight of the park-ranch boundary fence. At each site in park or ranch, three relevēs (10 m X 10 m) were established, two in grass communities and one in a shrub community. Two relevēs were established in the grassy areas of each site in order to preclude the possibility of the vegetation of one relevē being nonrepresentative of the site as a whole.

The vegetation was stratified into grass and shrub communities; grass communities by definition had at least 50% grass cover, and shrub communities should have had at least 50% cover of shrub species. However, several relevēs had shrubs covering only 40% or even 30% of the area even though the site

appeared to be dominated by shrub species. A shrub was defined as a woody plant below 2 m in height.

The two replicate grass community relevēs at each site were placed approximately 10 m apart. All relevēs were 10 m X 10 m in size. A relevē of 100 sq may be considered to fulfill the minimal area requirements for typical grassland communities (Mueller-Dombois & Ellenberg 1974). A baseline was laid out in a north to south direction from which five transects were run at right angles.

Vegetation sampling in the grassland relevēs was accomplished using a point frequency frame (Mueller-Dombois & Ellenberg 1974). This frame was 1 m long and 1 m high and carried five metal points. The frame was held upright and only the first interception of vegetation by the point was recorded. The point frequency frame was moved along the five transects of each grassland relevē, resulting in a total of 250 points per relevē. At each point the species struck was recorded, and at every other point the height of the plant was measured in centimeters. Rock, bare soil, litter, and cattle feces were recorded in the same manner as plant species in the sampling. Percentage cover for each species in a relevēs was determined from the 250 sample points.

Sampling procedure in the shrub relevēs varied somewhat from that of the grass communities. When the shrubs were below a meter in height, the point frame was used. Otherwise, a line marked every 20 cm was run down the transect through the shrubs, and a pole was lowered to the line at each mark to determine the cover above each sampling point. When the transect crossed shrubs in impenetrable thickets, the cover was estimated according to the width of the thicket. Heights of the shrubs were measured at every other point.

Soil sampling.--At each site one soil pit was dug within the previously sampled grassland relevē. The total soil depth and depth of each horizon were noted. At the same time, the fresh soil color of each horizon was determined using a Munsell color chart. Soil samples for later analysis were taken from the center of each horizon of the soil pits and placed in plastic bags. Soil depth at each site was sampled 50 times using a soil probe slightly over 1 m in length. This depth sampling was carried out within the two grass community relevēs of each site. Although surface rocks were avoided, an attempt was made to sample the soil depths throughout the two relevēs. A limitation of this method is that the striking of isolated rocks below the soil surface may lead to the underestimation of soil depth. In order to determine the bulk density of the soils, soil core samples were taken from the grass community relevēs of each site.

Analysis of Aerial Photographs

Two sets of aerial photographs of Hawaii Volcanoes National Park and adjacent lands were examined. The earliest set of photographs was taken in 1954, six years after cattle grazing ceased in the National Park. The second set of aerial photographs was made in 1965. These aerial photographs were used to determine changes in the vegetation structure of the mountain parkland over the 11 year span. The main objective was to compare the changes in tree and shrub cover within the park with those that may have occurred in the adjacent ranch.

A strip of the parkland ecosystem along the park-ranch boundary line was blocked off in both aerial photographs. The park and ranch portions of this strip were of equal size. This strip was 12 cm wide and 47 cm long in the 1954 photograph, which had a scale of 1:12,000. For the 1965 aerial photograph, with a scale of 1:17,000, a strip 8 cm X 32 cm was blocked off. Within each strip, the crown cover of trees was traced from the photograph onto a clear plastic sheet. A clear plastic overlay with a grid of points was used over the tracing of trees. The number of points striking trees was recorded for both the park and the ranch portion of the strip. The same grid of points was used for tracings of both the 1954 and 1965 photographs. A conversion factor dependent upon scale was calculated for each aerial photograph. According to this factor, the points that struck trees were converted into acres of cover. Tree cover could then be determined as a percentage of the total acreage in the park or ranch block.

Trees were easily recognized in the photographs, but no distinction was made between species. It was assumed that most of the trees were koa, but a few mamane and tall Dodonaea sandwicensis (a'ali'i) were undoubtedly included. More recent lava flows and vegetation types with Metrosideros polymorpha ('ohi'a) as the dominant species were excluded from the cover survey. These areas of different substrate and vegetation were quite recognizable in the photographs.

Shrub cover was determined directly from the aerial photographs using the tree cover overlay and the plastic grid of points. The process of converting points into percentage cover was the same as used for tree cover.

Soil Analysis in the Laboratory

Physical properties. Bulk density of the parkland soils was determined using the core samples obtained in the field, which were dried in an oven at 105°C. The dry weight (in grams) of the cores divided by the volume (in cubic centimeters) of the coring device resulted in values for bulk density. Porosity or percentage total pore space was calculated using values of bulk density and a standard value for particle density of 2.65 g/cm . The following equation (Vomocil 1965) was used: 100 x [(2.65 - bulk density)/2.65]. In addition, the texture of soils from selected sites was analyzed. The Bouyoucos method (utilizing a hydrometer) was employed to determine the textural class of these soils (Foth & Turk 1972). Also, the color of air-dried soil samples was determined using the Munsell (1954) color charts.

Other physical parameters examined included the field capacity and permanent wilting percentage of the sample soils. The field capacity of a soil is considered to be the upper limit of soil-water retention. The permanent wilting percentage is the lower limit of water availability to plants. Pressure plates at 0.3 bar (4.8 pounds/square inch) and 15 bars (220 pounds/square inch), respectively, were used to approximate these soil-moisture constants. Air dried soil was passed through a 2 mm sieve, packed into rings on ceramic pressure plates, and soaked overnight. Three subsamples of each soil were treated in this manner. The pressure plate apparatus was run until water loss from the plate became constant (generally for two days); then soil samples were weighed, oven dried, and weighed again. Percentage water content (gravimetric) was calculated for each subsample. This laboratory technique utilizes the standard pressure approximations of soil-moisture tension at field capacity and permanent wilting point (Foth & Truk 1972). The soil-moisture tensions at field capacity and permanent wilting point are known to vary with the soil, environmental conditions, and the plant species concerned, and are thus only approximated here.

Chemical properties.--The percentage organic carbon of a soil sample from each site was determined using the Walkley-Black method (Allison 1965). This analysis was run using 0.1 g of air-dried sieved soil with three subsamples selected from each sample. Soil sample pH's were measured with a Beckman pH meter using the paste method (soil and distilled water). Extractable amounts of phosphorus, potassium, calcium, and magnesium in the soils were determined by the Soil Testing Service of the University of Hawaii-U.S.D.A. Cooperative Extension Service. Estimations of pounds per acre of these four nutrients were made using a rapid turbidometric or colorimetric method. These results were then converted into fertility levels. As this method determines the amount of nutrient extracted from the soil, it is not an accurate measure of the total nutrient content or availability of nutrients to plants.

Data Processing

Percentage plant cover data were processed using two classification techniques. Two-way synthesis tables ordinating species into groups were produced through a computer program (Ceska & Roemer 1971). The cover data recorded in the field were converted into the Braun-Blanquet cover-abundance scale (Braun-Blanquet 1932). In this program both relevēs and species were classified. Relevēs were arranged according to the similarity index of Sorensen (ISs), which is based on the presence or absence of plant species. This index is calculated by the formula: $Is_S = 2c/(A+B) \times 100$ (Mueller-Dombois & Ellenberg 1974). In this formula c is the number of species common to two relevēs, A is the number of species in relevē A, and B is the number of species in relevē B.

The objective of this technique is the production of a final synthesis table exhibiting groups of differential or diagnostic species for the sample stands or relevēs. These differential species are those which differentiate the group of relevēs in which they occur from all other relevēs. Thus they distinguish their relevē group as a subdivision of the entire set of relevēs (Mueller-Dombois & Ellenberg 1974). Diagnostic species belonging to a group must conform to Rule I of Ceska and Roemer (1971), which states that the species must occur in at least X percent of the relevēs belonging to the relevē group and in not more than Y percent of the relevēs outside this group. Five sets of these threshold values (relating to Rule I) were used in this program: 50/10, 50/20, 66/10, and 66/33. Of these the 66/10 and 50/10 options are the more discriminating. Rule II was also applied, including a site into the species group if it contains X percent of the species associated with the group. The X percent of the two rules must always be the same (Ceska and Roemer 1971). Species of above 66 percent constancy were not considered for diagnostic (or differential) species. Utilizing the five options (or threshold values) mentioned above, five different synthesis tables were produced using the same data.

The second technique employed in the vegetation analysis was the dendrograph, by which the clustering tendencies of the sample stands or relevēs were examined. The relevēs may be clustered using indices of community similarity based on the plant species found in the relevēs. Again a computer program (McCammon & Wenniger 1970) was utilized to produce dendrographs based on similarity indices. Five similarity indices or community coefficients were used to produce five different dendrographs. The following formulae, along with others, were summarized and explained by Mueller-Dombois and Ellenberg (1974). Similarity indices involved in this program included Jaccard's index ($IS_J = c/(a+b+c) \times 100$). Gleason's quantitative modification of Jaccard's index ($IS_G = Mc/(Ma+Mb+Mc) \times 100$), Spatz's quantitative modification of Jaccard's index ($IS_{SP} = \leq(Mw:Mg)/(a+b+c) \times Mc/(Ma+Mb+Mc) \times 100$) Sorensen's index based on presence-absence ($IS_S = 2c/(A+B) \times 100$), and Motyka's quantitative modification of

Sorensen's index ($IS_{MO} = 2\leq Mw/(MA+MB) \times 100$). The following is an explanation of the symbols in the preceding formulae: IS = index of similarity, a = number of species found only in stand A, b = number of species found only in stand B, c = number of species common to stands A and B, A = total number of species in stand A, B = total number of species in stand B, Mg = greater quantitative value of a species common to stands A and B, Mw = smaller quantitative value of a species common to stands A and B. When M precedes the above symbols, this refers to the sum of the quantitative values of the species.

The percentage value derived from any of these similarity indices indicating the similarity of communities or sample stands was converted into a distance value by the computer. Using an arc cosine transformation (i.e., taking the cosine of the similarity index value), the computer converted high similarity values into low distance values and low similarity values into high distance values. In this way, the sample stands were arranged in a hierarchical manner according to the within-group similarity of the clusters of stands. As this program produced dendrographs rather than dendrograms, the between-group distance was also a factor in the production of the dendrograph.

RESULTS

Changes in Structure of Parkland Ecosystem

Using two sets of photographs, taken 11 years apart, the tree and shrub cover of a portion of the mountain parkland in the Hawaii Volcanoes National Park was determined. These findings were compared with the tree and shrub cover of an equal area within Keauhou Ranch directly adjacent to the Park. In 1954, just six years after the cessation of cattle grazing in the Mauna Loa strip, the tree cover within the Park was 4.4%, somewhat higher than the 2.5% tree cover found in the adjacent ranch. By 1965 the tree cover within the Park had increased to 10.3% and the tree cover of the section of the ranch had also increased to 3.2%.

Ground observations in the ranch near the boundary of the Park indicate that the differences between the tree cover in the Park and ranch may have been even larger in 1975 than in 1965. The few koa and mamane trees visible in this portion of the ranch appear to be quite decadent. No young trees have been observed in this area. By contrast, many young koa suckers and saplings have been observed from the Strip Road in the mountain parkland section of the Hawaii Volcanoes National Park.

The shrub cover within the Park was 17.5% in 1954 compared with 13.6% for the ranch. In 1965 both areas had increases in the cover of shrubs over 1954; the increase in shrub cover within the Park was greater than that in the ranch. The Park had 28.2%

shrub cover in 1965, and the ranch shrub cover was 19.7%. The principal species were Styphelia tameiameiae (pukiawe), Vaccinium reticulatum ('ohelo), Dodonaea eriocarpa, and D.sandwicensis ('a'ali'i).

Changes in Floristic Composition of Parkland Ecosystem

The differences in the floristic composition of the Park and ranch portions of the mountain parkland were considerable. The total number of species of higher plants found in the two areas was the same, the Park and ranch relevēs both showing 21 species. Each set of relevēs, though, had eight plant species not present in its counterpart. If the relative amounts (cover) of the species in Park and ranch are considered, the divergence in the vegetation of the two areas becomes even more apparent.

Examination of the list of the major plant species in the grassland relevēs of both the Park and the ranch reveals some obvious differences in the floristic composition of the two sets of relevēs (Fig. 2). The dominant grasses of the Park were Deschampsia australis and Holcus lanatus (velvetgrass). Deschampsia and velvetgrass rarely appeared in the ranch relevēs; Panicum tenuifolium, an endemic grass which occurred frequently in Park plots, was never observed in the ranch.

The most prominent grass species of the ranch were Sporobolus africanus (African dropseed), Axonopus affinis (narrow-leaved carpetgrass), Pennisetum clandestinum. (kikuyugrass), and Anthoxanthum odoratum (sweet vernal grass). Of these, carpetgrass and kikuyugrass never appeared in any Park relevē although the latter was observed growing by the roadside and along the boundary fence within the Park. African dropseed was found in only two Park relevēs, but sweet vernal grass was widespread in the Park. In fact, sweet vernal grass was practically ubiquitous in both Park and ranch as were Paspalum dilatatum, (Australian watergrass) and Eragrostis brownei (Brown's lovegrass).

The occurrence of forb species was less restricted than that of the grasses. Pteridium aquilinum var. decompositum (bracken fern), Rumex acetosella (sheep sorrel), and the ubiquitous Hypochaeris radicata (hairy catsear) were common to the ranch and Park. The native sedges, Carex wahuensis and C. macloviana (St. Malo's sedge) occurred only in Park relevēs, while Lotus angustissimus, Medicago sp. (trefoil) and Veronica plebeia (common speedwell) were only observed within the ranch.

The floristic composition of the Park and ranch shrub relevēs was also different (Fig. 3). The dominant shrub species of both ranch and Park relevēs was the indigenous pukiawe. Another native shrub, 'a'ali'i, occurred only in Park relevēs. The remaining plant species recorded in the shrub relevēs were much the same as those of the grass community relevēs. The same

differences and similarities in floristic composition of the Park and ranch appeared in the shrub relevēs. A notable exception was the frequent occurrence of the endemic Deschampsia in the ranch shrub relevēs. This grass was often found growing up out of the center of pukiawe shrubs, where it was presumably protected from grazing, being out of the reach of cattle.

Origins of Plants found in relevēs.--An examination of the list of grass species found in the study relevēs (Table 1) as well as species lists of Figures 2 and 3 reveals that most of the grass species occurring on the ranch are exotics. By contrast, the two native grasses occurred primarily in the Park. Most of these exotic grasses were introduced as range grasses in the early part of this century. Cynodon dactylon (Bermuda grass) was the earliest introduction on the list, arriving in 1835. Almost all continents are represented in the list as points of origin for these grasses.

The shrub species found in the study are all indigenous or endemic to the Hawaiian Islands. Likewise, the one fern and two sedge species are Hawaiian natives. Virtually all the other non-grass species in Figures 2 and 3 are exotics, mainly from Europe.

The relevē codes are derived from the site number (1-8), location in Park or ranch (P or R), and the relevē number. Relevēs numbered 1 and 2 are in Park grass communities, while relevē numbers 4 and 5 are replicates in ranch grasslands. Relevēs numbered 3 are in Park shrub communities and relevēs identified by the digit 6 are found in ranch shrub communities. A consistent pattern emerges from a comparison of the cover values of exotics and indigenes in Park and ranch relevēs at the same elevation (Table 2). In the Park relevēs as a whole, the percentage cover of native plants is approximately double that of the exotic plant species. This situation is reversed for ranch relevēs, where exotic species comprise more than double the percentage represented by indigenous or endemic species.

Clustering Tendencies of Relevēs

Classification of species and relevēs by two-way synthesis tables.--Of five synthesis tables produced by computer program (Ceska & Roemer 1971), one will be presented. The program had five options based on threshold values for species inclusion into the species group. Three of these options (namely those with threshold values of 50/10, 50/20, and 66/10 produced indistinguishable synthesis tables with a single identical species group.

The numbers within the synthesis table are those of the Braun-Blanquet cover abundance scale. In this study these cover values were not estimated; cover values from vegetation sampling were simply converted to the scale for use in the program.

However, the synthesis table program was actually dealing with the presence or absence of a species rather than with its quantitative value in the relevē.

Examination of the relevē codes along the top of the synthesis table (Table 4) reveals two groups of differential species; one species group is characteristic of the Park relevēs, while the other species group contains ranch relevēs exclusively. Relevē codes are the same as presented in Table 2, R indicating a ranch relevē and P denoting a Park relevē.

Species Group 1 is composed of three plant species (Deschampsia, velvetgrass, and Carex wahuensis) in 22 relevēs. Every Park relevē, with one exception, was assembled into this species group. Only one grass community relevē from the lowest site (4600 ft elevation) was omitted. This relevē could not be included in Species Group 1, as it lacked both Deschampsia australis and Carex wahuensis. Thus the relevē did not fulfill Rule II of the program, which requires a relevē to contain at least 66% (in this case) of the diagnostic species.

Considering the three species comprising Group 1, Deschampsia is an endemic Hawaiian grass, velvetgrass is a species introduced from Europe, and Carex wahuensis is an endemic sedge. Deschampsia did occur in a few ranch relevēs in relatively small amounts. The relevē numbers reveal that five of the seven ranch stands containing this grass species were shrub communities. Deschampsia was frequently observed growing in the center of low shrubs where it was apparently out of the reach of cattle. By contrast, this grass was absent from only one Park relevē. Velvetgrass, the second species of Group 1, was found in three ranch relevēs in rather insignificant amounts. However, this introduced species was a component of every Park relevē, without exception. Carex wahuensis, the third diagnostic species, was confined to the Park relevēs.

Species Group 2 is composed of five differential species which were characteristic of the ranch. Not one Park relevē appeared in the group, although all but two ranch relevēs were included. The two ranch relevēs that were omitted from the group were shrub stands at sites 4 and 6 (4R6 and 6R6). The shrub relevē at site 6 appeared to be quite dissimilar to the others included in this species group, lacking all four of the grass species of the group. The shrub relevē at site 4 had more in common with those of the species group as it contained three of the five diagnostic species of the group (two grasses and cattle feces). The four grasses that appeared in this diagnostic species group are all introduced ones: African dropseed, carpetgrass, Brown's lovegrass, and kikuyu grass. Of these four, African dropseed is considered a weed, while the others are useful to some extent as range grasses. Cattle feces is the fifth component of Species Group 2.

The remainder of the synthesis table also yields information about the area studied. Hairy catsear, sweet vernal grass, as well as litter, were consistently found in all relevēs. Thus they were of little value as diagnostic species. Other species occurred too rarely to contribute to species group formation. In fact, species such as Juncus tenuis and Bromus rigidus (ripgut grass) occurred only once in a single relevē.

This synthesis table excluded only three relevēs from membership in one of the two species groups. Two were ranch shrub relevēs, so only one Park relevē was omitted from the species groups. These relevēs were certainly unlike the others of the two groups, lacking several of their diagnostic species. Table 4 presents Deschampsia and velvetgrass as the dominant plants of the Park portion of the ecosystem, while African dropseed is seen to be the dominant grass of the ranch part of the study.

In essence, this synthesis table has demonstrated the floristic disparity of the two segments of the mountain parkland ecosystem separated by the Park-ranch boundary fence. Each of the two areas had its own set of differential or diagnostic species; all but three aberrant relevēs out of a total of 46 belonged to one of the two groups.

Analysis of vegetation by the dendrograph technique.--The dendrograph is a useful device whereby the relationships between relevēs in a classification scheme may be graphically illustrated. Dendrographs were produced through a computer program (McCammon & Wenniger 1970) using five different similarity indices. Two of these dendrographs will be presented. One dendrograph was based on the presence or absence of species in relevēs; the other utilized the quantitative values (cover) of species.

Jaccard's similarity coefficient for plant communities (Figure 4) involves the presence or absence of species without regard for species quantities. The numbers along the x-axis are the percentage within-group similarities. A line drawn across this dendrograph at just above 60% similarity isolates four clusters of relevēs. The line was established at 60% because the clusters occurring near the mid-range of similarities are more likely to be ecologically meaningful (Mueller-Dombois & Ellenberg 1974). Of the four clusters, two are composed entirely of Park relevēs, and two contain only ranch relevēs. Examination of the relevē numbers along the x-axis reveals that Group A is composed of 14 Park relevēs, including all seven shrub plots. The grass relevēs in this group are those of the upper sites. Group B likewise consists of Park relevēs, although the nine plots consitituting this group are all grass community relevēs. With one exception, the Group B relevēs belong to the lower four sites. Groups C and D are composed solely of ranch relevēs, but there is no distinction between grass and shrub community stands within the two groups. Group C has seven relevēs from sites 3,

4, 5, and 6, the mid-elevational sites. Group D is larger, including 16 relevēs representing every site except site 6. These four clusters have within-group similarities as follows: Group A, 64%; Group B, 61%; Group C, 64%; Group D, 63%. The dendrograph method using Jaccard's index of similarity (based on presence-absence) readily separates the Park and ranch relevēs and distinguishes between upper and lower sites within the Park. However, grass and shrub community relevēs appear in the same clusters.

In the dendrograph based on Jaccard's index there is absolutely no intermingling of ranch and Park relevēs; they are separated into two clusters between the 40 and 50% similarity levels. Other information of possible ecological interest to be gleaned from this dendrograph includes the grouping of Park shrub relevēs in the same cluster as Park grass relevēs of the upper four sites, as well as the separation into two clusters of the Park grass relevēs of upper and lower sites. These two sets of Park sites have apparently been separated on the basis of only a few plant species, as no drastic differences may be discerned from Figure 2 which presents species cover of grassland relevēs. As this dendrograph is based on presence-absence rather than quantity, species of low cover values were instrumental in effecting this separation of grass relevēs.

The grassland relevēs of the four lower sites in the Park did include several species not present in those of the four upper Park sites. In particular, Australian watergrass and sheep sorrel occurred in all but one of these relevēs but were not found in grassland relevēs of the Park's upper sites. It must be noted that sheep sorrel was observed in the upper reaches of the ecosystem but was never encountered in the Park relevēs at these higher sites. Other species whose distribution was limited to the lower sites were of more sporadic occurrence and included African dropseed, narrow-leaved plantain (Plantago lanceolata), willow herb (Epilobium cinereum), and a'ali'i. Again, it must be emphasized that these species may occur in the upper portion of the parkland; nevertheless, their presence was not recorded in the upper four Park sampling sites. Another species which may have affected the clustering pattern was bracken fern, which although not confined to lower elevations, was certainly more prevalent there. This dendrograph demonstrates that selective grazing pressure of cattle has resulted in the suppression of altitudinal variation in ranch grasslands of the parkland ecosystem.

As cover data were collected during the field work, a dendrograph employing a similarity index based on quantitative values would utilize more of the available information about the study area. Therefore, the dendrograph based on Motyka's quantification of Sorensen's index of similarity is presented (Fig. 5). Two lines have been drawn on this dendrograph at 60% and 51% within-group similarity, again in the mid-range of similarities. Line 1 at 51% similarity isolates three clusters

of relevēs. Cluster A is composed of 13 grass community relevēs from the Park portion of the study area. The within-group similarity of this cluster is 61% The relevē numbers of Cluster B reveal that all 13 members of this group are from shrub communities. Both Park and ranch relevēs are included in this cluster, whose within-group similarity is 67%. Cluster C is the largest of the three groups, containing 20 relevēs, 17 from the ranch area and three from the Park. All but one of these 20 are grass community relevēs. The within-group similarity of this cluster is 59%.

A second line is drawn across the dendrograph at 60% similarity. Line 2 isolates four clusters of stands, two of which are identical to Clusters A and B isolated by line 1. However, Cluster C of line 1 becomes Clusters c and d of line 2. Cluster c contains three grass community relevēs of the Park, and Cluster d is composed of 16 grass community relevēs and one shrub relevē from the ranch half of the study. The within-group similarities of Clusters c and d are 76% and 66% respectively. It is interesting to note that this dendrograph technique completely separates the Park and ranch grass community relevēs. The shrub community relevēs are grouped together regardless of their origin. This is probably due to the fact that the dominant shrub species of these relevēs were the same in both areas. The grass component of the shrub relevēs was not large enough to greatly affect the cluster formation. The fact that the shrub species a'ali'i occurred in a couple of Park relevēs but was absent from the ranch did not alter the clustering of shrub relevēs.

It may also be assumed from this dendrograph that shrub relevēs have more in common with Park grass relevēs than with those of the ranch, according to the proximity of the two clusters on the x-axis. The ecological reasoning behind the isolated cluster of three Park grass relevēs, which is nearer the major ranch cluster than the cluster of remaining Park grass relevēs, is somewhat obscure. Also difficult to explain is the inclusion of one ranch shrub relevē in the cluster which is otherwise populated by ranch grass relevēs. One possible reason for this placement is the low percentage cover of pukiawe, the dominant shrub in this aberrant relevē.

Referring to the dendrograph of Figure 5, higher levels of within-group similarity yield somewhat less information. A line at 70% similarity would isolate nine clusters of relevēs. Five of these clusters are comprised of Park grass community relevēs, and two clusters include all the ranch grass community relevēs. The remaining two clusters are composed of shrub relevēs. With the exception of the clusters of shrub relevēs, there seems to be little ecological significance to the clusters at 70% similarity. Even less importance may be attached to the clusters which appear at 80% within-group similarity. At this level 20 groups exist, 11 of which contain only one relevē.

The diagram of Figure 5 further illustrates the position of the line 2 dendrograph clusters along the elevational gradient. The Park sites appear on the right and the ranch sites are on the left portion of the diagram, indicating low variation in relevēs along the elevational gradient. According to this dendrograph, the relevēs of the mountain parkland grass communities are grouped together on the basis of their location in either the Park or ranch.

The second dendrograph (Fig. 5), based on Motyka's quantitative revision of Sorensen's similarity index, differs somewhat from the one based on presence-absence data. The Park and ranch relevēs are not so completely separated. As in the previous dendrograph, the first separation of clusters appears near the 40% similarity level. Unlike the Jaccard dendrograph, some representatives of both study areas are included in the two major clusters.

The two dendrographs presented also differ with respect to altitudinal variation among relevēs. The dendrograph according to Sorensen's quantitative index does not exhibit clustering of relevēs on the basis of their position on the altitudinal gradient, as does the dendrograph based on the presence-absence index of Jaccard.

Other dendrographs examined include those produced using the indices of Spatz and Gleason. Both of these indices are quantitative modifications of Jaccard's index of community similarity. The dendrograph based on Gleason's index was of little use, as the only two levels of within-group similarity appearing along the y-axis were 80 and 90%. This indicates a very high degree of relevē homogeneity, which was not borne out by the other dendrographs. Such homogeneous clusters are not conducive to ecological interpretation.

The dendrograph based on the Spatz index of similarity exhibits clustering tendencies quite different from those of the Gleason index dendrograph. The levels of within-group similarity falling in the mid-range isolate many groups composed of only one or two relevēs. This situation creates difficulties in analyzing the significance of the clusters. Three relevēs were located at each Park or ranch site, thus this method tends to separate replicate stands into different clusters. The three dendrographs which are not presented here may be found in Appendix II.

In summary, both of the dendrographs presented here have four main clusters of relevēs at the 60% level. The dendrograph based on Jaccard's presence-absence index completely separates Park and ranch relevēs, as Park stands comprise two clusters and those of the ranch make up the remaining two major clusters. Another accomplishment of this dendrograph is the clustering of lower elevational Park grass communities apart from the upper Park grass communities with the inclusion of Park shrub relevēs in the latter group. The dendrograph resulting from the use of

Motyka's quantification of Sorensen's index affects a less than total separation of Park and ranch vegetation, as shrub relevēs of both Park and ranch are grouped together in one cluster. The three remaining major clusters of this dendrograph are composed of most Park grassland relevēs, three aberrant Park grassland stands, and all ranch grass community relevēs plus one ranch shrub stand. The two dendrographs presented have one thing in common; both segregate park and ranch relevēs to some degree, although the degree of separation varies.

A Comparison of Ranch and Park Soils

The soils of the mountain parkland ecosystem are andept Inceptisols, which are soils of recent origin having horizons. Andept implies the presence of volcanic ash or pumice in the soil. Parkland soils were formed from shallow ash deposits over both aa and pahoehoe flows. The two most prevalent soil series of parkland soils are Hanipoe and Apakuie, which are quite similar. Both series are well-drained soils formed in volcanic ash of upland areas, but the two soil series differ somewhat in texture and acidity. Apakuie soils are sandy loams with a neutral pH, while Hanipoe soils are silt loams or loams which are slightly acidic. The two types of Hanipoe soils occurring in the study area differ in their stoniness and depth, HCD soils being shallower and containing more loose surface stones than the soils designated HDD in the soil survey of Sato et al. (1973).

According to soil maps of the most recent soil survey (Sato et al. 1973), the study plots were all located on soil types of one of the two series described above. The soil types of the paired sites were very similar (Table 5). As the paired sites of Park and ranch were relatively close together, one would expect the climate to be equivalent in the two areas. The previously presented vegetation analyses are evidence that the present plant cover of the Park and ranch study areas differs greatly. However, these changes in vegetation are thought to be relatively recent. The following results of examination of physical and chemical properties of soils will indicate the magnitude of the similarities and differences of the soils of the Park and ranch relevēs.

Physical properties of soils.--Soil pits dug in one grass relevē at every site revealed the horizon development of the soil. At all eight Park sites two horizons appeared. The upper or A horizon was generally darker brown in color than the B horizon, and the two were typically separated by a band of reddish hue. At half the ranch sites only one horizon could be distinguished, while the other four sites showed horizons much like those of the Park soil pits. The soil samples from the ranch sites showing only one horizon were considered to be from the A horizon. Data concerning horizons collected from the soil pits may be found in Appendix III.

Soil depth.--Fifty soil depth measurements were taken in grassland sites in the Park and ranch. The mean soil depths of Park sites and ranch sites are presented in Figure 6. At all but two elevations the Park soil depth was considerably greater than that of the ranch. The results of a t-test revealed a significant difference in the ranch and Park soil depths at the 99% confidence interval.

Soil depth also changed with elevation (Fig. 6), and a definite trend of decreasing depth with increasing elevation was observed. The pattern for ranch depths was less regular with peaks of mean soil depths at the lowest and middle elevations. Fluctuation in mean soil depth at different sites within the mountain parkland is understandable as the soil parent material consists of ash deposits of variable thickness.

Bulk density, soil texture, and porosity.--Results from calculation of bulk density (weight per unit volume of dry soil) were somewhat surprising. As compaction of soil leads to higher bulk density, it was presumed that ranch soils compacted by the hooves of cattle would have higher bulk density values than corresponding Park soils. This, however, was not the case (Fig. 7). With one exception, bulk densities of Park soils were higher than those of the ranch soils. All of these bulk density values were remarkably low, indicating that the mountain parkland soils are porous and loose. However, no statistical test was carried out to determine the significance of this difference in Park and ranch soil bulk densities, because replicate cores were not taken during field sampling. As fewer than four cores per site may result in unreliable bulk density values, the disparity in bulk densities may not be significant.

Soil texture, the relative size of soil particles, is related to bulk density. Generally, coarse-textured soils have higher bulk density values than fine-textured soils. The textural classes of these mountain parkland soils indicate their relative coarseness (Table 6). This coarseness in texture does not correlate with the low bulk densities of parkland soils. The figures for percentage clay (Table 6) also ran counter to the bulk density results. As Park soils had higher bulk density values, one might expect a smaller percentage clay in these soils, compared with those of the ranch. However, just the opposite relationship was exhibited by the results of this textural analysis.

Another parameter closely related to bulk density is porosity or percentage total pore space. Porosities of Park and ranch soils were calculated using values of bulk density. Values of the calculated porosity for Park and ranch soils were quite similar and showed a high percentage of pore space (Table 7).

Soil moisture retention properties.--Two soil moisture constants were determined for each soil sample: field capacity and permanent wilting percentage. These two values are

characteristic of the soil sampled, relating to soil texture and structure. Field capacity is defined as the amount (in this case, weight) of water held in the soil after gravitational water has drained away and the rate of downward movement of water has become very slow. The permanent wilting percentage is the amount of water in soil when permanent plant wilting occurs. Both values have ecologic importance: in general, the field capacity is the upper limit of water availability or storage, and the permanent wilting percentage is the lower limit of available water for plants.

The field capacity of soil from each horizon of every site was approximated using the laboratory technique described earlier. The water content values presented in the following figures are the means of three subsamples of every soil sample. With the exception of one site, the percentage moisture in A horizon soils at field capacity ranch soils held more water than Park soils (Fig. 8). A t-test indicated that this difference was significant at the 0.01 level. The moisture content of A horizon soil of the ranch relevē at 5800 feet elevation (site 7) seems extreme in relation to all other values, although it corresponds to the moisture retention at 0.3 atmosphere reported for Apakuie soils by Sato et al. (1973). The percentage moisture values for B horizon soils at field capacity for the ranch soils were considerably higher than those of the Park soils (Fig. 9). Again a statistical test supported the hypothesis that the differences between Park and ranch soils were significant at the 0.01 level.

The second soil moisture constant, permanent wilting percentage, was approximated using the same laboratory technique as was used to determine soil field capacity. The permanent wilting percentage (water content at permanent wilting) of A horizon soils of both Park and ranch is shown in Figure 10. A comparison of this figure with Figure 8 reveals that trends in water content at permanent wilting followed those of water content at field capacity. As with field capacity, water content at permanent wilting was greater for ranch soils than Park soils. At only two sites was the percentage moisture value larger for Park soils. This difference was significant at the 0.01 level according to a t-test. Again the water content of A horizon soil of the ranch releve at 5800 feet elevation seems disproportionately large and may be due to some error. As with the A horizon soils, the permanent wilting percentages of the B horizon was greater for ranch relevē soils than for those of Park plots (Fig. 11). This difference was significant at the 0.05 level, as determined by a statistical t-test. It may be noted that the water holding capacity (or amount of water in the soil between field capacity and permanent wilting point) was about the same in ranch and park soils. So despite the higher percentage water retained by ranch soils under pressure approximations of the two soil constants, the water available for plant use appeared to be equivalent in the two areas.

Chemical properties of soils.--Chemical properties of soils investigated included pH, nutrient content, and percentage organic carbon. As the organic carbon results seem to have some bearing on the findings presented in the section on physical properties, they will be considered first.

Organic carbon.--These values were determined by the Walkley-Black method as discussed under Methods. At every site except one, the percentage organic carbon was considerably higher in the A horizon of ranch soil than the corresponding Park soil (Fig.12). This difference was significant at the 0.01 significance level by a two sample t-test. In the ranch soils there seemed to be a trend toward higher percentage organic carbon with increasing elevation. This is reasonable, as the breakdown and decomposition of organic material is slower at lower temperatures. However, no similar trend was exhibited by the values for the Park. The organic carbon values for Park soils were extremely variable, ranging from a low of 0.71% to a high of 8.65%. This variability is difficult to explain, since all Park soil samples were taken from grass communities of the same basic plant species composition. Pig digging in the Park may have been partly responsible for these inconsistent results, as such activity would bring about the mixing of horizons and the upturning of deep soil containing less organic matter.

The results of organic carbon determinations for B horizon soils (Fig. 13) show that values for ranch soils were much higher than those of Park soils. At only one site was the percentage organic carbon of the ranch soil lower than that of the Park soil. Again this difference in Park and ranch soils was significant at the 0.01 significance level according to a two sample t-test. As with the A horizon soils, percentage organic carbon varied greatly with the site sample. Because of the site variation displayed by the graphs of Figures 12 and 13, a comparison of organic carbon values for A and B horizons was difficult. The organic carbon means for A and B horizons of all Park soils were quite similar, being 3.29% and 3.47% respectively. This greater value for B horizon soils was unexpected, as deeper soils typically have less organic matter than the soils above them. Means of organic carbon values of A and B horizons of ranch soils were 8.77% and 6.81% respectively. Statistically the differences in organic carbon of A and B horizon soils were not significant for either Park or ranch sites.

pH.--The soils of the mountain parkland ecosystem were moderately to slightly acidic. pH values ranged from 5.5 to 6.6. At six of the eight sites the pH values for A horizon soils of ranch soils were more acidic, as indicated by lower pH values (Fig. 14). This difference was statistically significant at the 0.05 level. A comparison of the pH values for B horizon soils of Park and ranch graphs reveals lower pH values for ranch soils (Fig. 15). Again this difference was significant at the 0.05 level according to a two sample t-test. pH values were slightly

higher in B horizon soils as compared to A horizon soils (Fig. 14,15), but this difference was not statistically significant. There was no definite correlation between pH and elevation.

Nutrient analyses.--Park and ranch soils were analyzed for extractable amounts of four nutrients: calcium, potassium, phosphorus, and magnesium. All four are macro-nutrients essential in relatively large amounts for plant growth. The amount of each nutrient extracted from the soil sample in pounds per acre has been converted into fertility levels (Fig. 16,17). There seemed to be little variation in the amount of the level of fertility of all four nutrients present in the A horizon soils of Park and ranch soils (Fig. 16). There was also very little change in the fertility level of any of the four nutrients with elevation. The amount of phosphorus and magnesium was found to be very low at every site in Park and ranch. This is not surprising, as phosphorus is generally not found in large amounts in soils. Calcium seemed to be plentiful in all but one plot. Likewise, potassium was present at moderate to high levels at all but two sites. These results indicated that fertilizer has not been applied to the pasture soils in the recent past, as ranch and Park soils were so similar in their content of the four nutrients. Therefore with regard to nutrient availability (as was true for soil water), plant growth should be similar in Park and ranch relevēs.

Fertility levels of these four nutrients in B horizon soils are shown in Figure 17. Again phosphorus and magnesium were present at a very low level in all Park and ranch soils sampled. A comparison of this figure with Figure 16 reveals that levels of calcium and potassium were generally lower in B horizon soils than in the A horizon soils of the same plot. There was little difference in the nutrient levels of B horizon soils of Park and ranch relevēs. Fertility levels were not radically different at the eight elevations, although the soils of the two upper Park relevēs did have a lower level of calcium than those of the other Park relevēs. As with A horizon soils, there was no definite correlation between level of nutrient present and elevation. The actual amount of each nutrient extracted from the soils in pounds per acre determined by turbidometric and colorimetric techniques is listed in Appendix III.

Correlation of Vegetation and Soil

The results of both forms of vegetation analysis revealed great disparity in the vegetation of the Park and ranch relevēs. The results of soil tests and field examination also showed some differences in the two areas, although these dissimilarities were less pronounced. There appeared to be little direct correlation between the two sets of results, but one fact was clear: the soils of the two areas differed less than the vegetation.

Structural differences between Park and ranch were a matter of degree, with the Park showing a greater percentage cover of both trees and shrubs. The vegetation of the two study areas was floristically quite distinctive, with exotics predominating in the ranch and endemic grass species prevalent in Park relevés. The quantitative values of the species common to both areas were also dissimilar. These differences were apparent in the results of the clustering techniques presented in an earlier section. The synthesis table presented indicated that each of the two areas had a diagnostic species group peculiar to it: the Deschampsia-Holcus-Carex group in the Park and the Sporobolus-Axonopus-Eragrostis-Pennisetum-cattle feces group in the ranch. Likewise, the dendrographs presented in a previous section exhibit clustering of relevés on the basis of their location in either the Park or ranch. Using these techniques, the differences in the vegetation of the two areas studied have been established.

Results of field and laboratory examination of the soils of the two study areas revealed both similarities and differences. The soils were superficially similar and differed little with regard to soil type, textural classification, soil color, and horizon development. This was to be expected as the soils of both Park and ranch were derived from the same parent material.

Dissimilarities appeared in both the physical and chemical properties of the soils. The soils of the Park relevés were deeper than those of the ranch, but this variation in soil depth cannot be directly correlated to any adverse effect of cattle grazing. No serious erosion was observed in ranch pastures during this study. The most likely explanation for this disparity is that the variable soil depths are a function of the soil parent material, derived from discontinuous ash deposits. Soil depths were not measured in the shrub relevés, but one observation may be mentioned concerning these communities. During fieldwork it was noted that areas with the highest shrub cover were frequently rough with rock outcroppings. In fact, these communities often occurred on rocky ridges, a phenomenon previously reported by Mueller-Dombois (1967). As the selection criteria for shrub relevés included relative levelness, placement of shrub relevés was more difficult than that of their grassland counterparts. The percentage of area covered by rocks in the ranch shrub relevés was found to be over 4% on the average. This was more than double the mean percentage cover of rock in the shrub relevés of the Park or in either set of grassland relevés. The soils of the ranch shrub communities were thus the most rocky of any soils investigated in study.

As reported in the previous section, the percentage moisture at field capacity and permanent wilting point were both considerably higher in the soils of the ranch relevés than in those of the Park relevés, despite the fact that the soil textures were similar in the two areas. As soil moisture constants are characteristic of the soil studied, these results

emphasize the aspect of dissimilarity of the soils of the two study segments. It is known that the presence of organic matter increases the water-holding capacity of a soil and also decreases the bulk density. So the previously presented results of organic carbon analysis, reavealing that the ranch soils contained a higher percentage of organic carbon than the soils of the Park relevēs, are consistent with the soil moisture and bulk density results.

The percentage of area covered by litter was higher in the ranch relevēs than in those of the Park. The average percentage cover of litter was 31.75% in the grassland areas of the ranch and 23.7% for the Park grass communities. The observation of greater litter cover in the ranch may have been a function of the point intercept method of vegetation analysis. The lesser height of ranch grasses permitted the point of the frame to penetrate to the litter layer before achieving a strike. The tall grasses and inflorescences of the Park made the interception of litter concentrated at ground level more unlikely. This abundance of litter, as well as the presence of cattle feces in the ranch sites, may have contributed to the higher organic carbon levels of the ranch soils. Cattle feces accounted for 2.89% of the mean cover of the ranch relevēs.

In addition to the results concerning water-holding capacity, two factors indicated that ranch soils may be capable of retaining moisture better than Park soils. As mentioned above, the litter cover was greater in the ranch than in the Park. Also the area of exposed soil was greater in the Park relevēs and 2.98% for the ranch relevēs. Pigs digging for bracken fern rhizomes and hairy catsear leaves in Park grasslands were probably the cause of the greater amount of exposed soil in this area. These two factors of litter cover and exposed soil surely influence the speed and amount of evaporation of moisture from the soils of the mountain parkland.

Another soil property which may possibly be related to vegetation cover is pH. Results presented earlier showed that the ranch soils were more acidic than those of corresponding park areas. As the soil acidity may be influenced by the decomposing plant litter of the area, the differing flora of the ranch and Park might conceivably be responsible for the variance in soil pH. This is merely speculation, as no data are available to indicate that ranch plant species are more inclined to acidity than those growing in the Park. One other factor which certainly has contributed to greater acidity in the ranch soils is the higher level of organic matter.

Percentage organic carbon was thus the pivotal soil factor of this study; it was the one soil property which seemed to show a correlation with the other soil properties investigated (Table 8). There was a negative linear correlation between pH and organic carbon and between bulk density and organic carbon. This implies that the pH and bulk density of parkland soils decreased

as the organic carbon increased. The correlations between organic carbon and water content at both field capacity and permanent wilting percentage were positive and high for A horizon soils and somewhat lower positive values for B horizon soils.

The soils of the ranch and Park relevēs were rather dissimilar in both physical and chemical properties, although they were related by their origin and development. The vegetation differences of the two areas cannot be considered responsible for the differing soil results. Conversely, it cannot be inferred that the vegetation of the ranch and Park portions of the mountain parkland differed due to edaphic factors. The conclusion presented here is that the vegetation has been altered by cattle grazing while the soils have escaped the potentially detrimental effects of grazing. The differences in soil properties of the two areas may be attributed to the higher percentage orgainc carbon in the ranch. The mechanism behind the organic carbon accumulation in ranch soils is obscure but may indicate the involvement of differing rates of microbiological activity in the soils of the Park and ranch. Another possibility is that these results are evidence of a very subtle influence of the disparate vegetation cover acting upon the soil through the process of litter decomposition.

DISCUSSION

Daubenmire (1940) has stated that, "In any study of the grazing factor, one must have evidence that the original vegetation was essentially identical at all the stations which are analyzed and that the environment, except for the herbivores, was uniform." Although it is impossible to demonstrate that the two areas studied were previously identical, the proximity of the Park and ranch sites makes this a distinct possibility. In any case, the fence line separating the Hawaii Volcanoes National Park and Keauhou Ranch is not a natural boundary. For evidence of the vegetation of the mountain parkland ecosystem before the advent of introduced mammals, there are descriptions of the vegetation observed during ascents of Mauna Loa by both Menzies in 1794 (Menzies 1920) and Douglas in 1834 (Wilson 1919). Although uniformity of the environment for any two sites is difficult to establish, the placement of the pairs of relevēs insures similarity in the climate of the sites. Soil pits at each site indicate a similarity in the soil parent material and horizon development.

Vegetation Structure

Even a cursory examination of the ranchland adjacent to the mountain parkland ecosystem of the Hawaii Volcanoes National Park reveals remants of the former vegetation. At the lower

elevations of the former ecosystem, old and decadent koa trees are not uncommon. Near the middle of the parkland, at elevations near 5600 feet, mamane trees occur on the ranch. No young trees, saplings or seedlings of these two native species were observed during the study of this region of the ranch.

Results from a comparison of two sets of aerial photographs of the parkland ecosystem emphasized the differences in the vegetation structure of the two areas. The tree cover of the part of the mountain parkland within the Park more than doubled in the 11 year interval between aerial photographs. During this same time the percentage cover of trees in the ranch adjacent to the Park increased only slightly. This increase in Park tree cover was mainly due to the spread of koa colonies. Mueller-Dombois and Krajina (1968) calculated that these colonies of koa were penetrating the mountain parkland grasslands at a rate of 0.5-2.5 m per year.

This expansion of koa in the absence of cattle supports the conclusions of Baldwin and Fagerlund (1943) who maintained that cattle grazing suppressed koa reproduction. This suppression resulted in an alteration of the natural vegetation structure of the parkland ecosystem. Since removal of cattle from the Mauna Loa Strip of the Hawaii Volcanoes National Park in 1948 (Apple 1954), the grazing pressure has been diminished while cattle have continued to graze in the Keauhou Ranch. Thus the structural degradation of the ecosystem continued in the ranch portion of the study area while the Park portion began to recover.

The increase in Park tree cover has occurred despite the presence of feral goats in the ecosystem. It is evident from a parkland exclosure study by Spatz and Mueller-Dombois (1973) that goats may seriously impair the vegetative reproduction of koa by browsing. Feral pigs present in the mountain parkland ecosystem may also be responsible for damaging young koa seedlings (Scowcroft 1971; Cooray 1974). However, the combined impact of these feral animals seems to be less important than the effects of cattle grazing on the structure of the vegetation of this ecosystem. Bryan (1971) has remarked that cattle have done more damage to the native Hawaiian flora than all the other introduced factors, such as sheep, goats, insects, diseases, and man-made fires.

It must be noted that the both goats and pigs occur in the ranch portion of the mountain parkland as well as in the Hawaii Volcanoes National Park. The Park has made an effort in recent years to reduce goat and pig populations through hunting, while this type of consistent control is largely lacking on the adjacent ranch. The author has on several occasions observed goat herds on Keauhou Ranch numbering between 30 and 40 individuals.

The aerial photographs also revealed an increase in shrub cover in both Park and ranch between 1954 and 1965. The

percentage of area covered by shrubs increased by 11% in the Park and by 6% in the ranch portion of the study. The increase in both Park and ranch indicates that fluctuation in the numbers of cattle grazing in the ranch may be a factor to be considered. Also, a cessation or reduction of the ranch practice of clearing shrubs may be involved in the increase in ranch shrub cover. Indigenous shrubs such as 'a'ali'i and pukiawe are considered to be noxious plants because of their lack of forage value (Hosaka & Thistle 1954). It is known that shrub clearing was practiced on Kapapala Ranch prior to 1948 (Apple 1954); it is possible that a reduction in this activity is responsible for the shrub cover increase noted on Keauhou Ranch. Cattle undoubtedly do graze upon shrubs in the ranch even though the most common shrub of the area (pukiawe) has small prickly leaves and is probably less palatable than other plants of the area. During this study it was noted that many ranch shrubs had a rounded, clipped appearance. The height of shrubs was consistently greater in Park relevēs (Appendix II).

A frequent effect of cattle grazing noted in North America is the increase of shrubs at the expense of grasses (Clements 1949; Johnston et al. 1971). This does not seem to be the case in the mountain parkland ecosystem. Although the shrub cover did increase in the ranch, this increase was probably localized in the rocky areas which are the normal habitat of shrub communities (Mueller-Dombois 1967). Thus the shrub cover increase did not represent an encroachment upon grass communities. It is not uncommon for cattle to cause drastic changes in the vegetation cover. In New Zealand cattle and other feral animals converted a rain forest into a grassland (Moore & Cranwell 1934). Forests in temperate climates may also be reduced to grasslands solely through the grazing of animals (Cloudsley-Thompson 1975). Nevertheless, structural degradation of vegetation may not be permanent if the grazing is discontinued. Cockayne (quoted by Allan 1936) believed that removal of grazing animals from areas of New Zealand would enable pastures to revert to rain forest.

The capacity of cattle to alter the structure of vegetation is well established (Adams 1975). In the mountain parkland, cattle grazing may cause the decrease of the tree stratum by interfering with tree regeneration (Baldwin & Fagerlund 1943; Whitesell 1964). Another reported consequence of cattle grazing is the destruction of trees by root trampling. Koa trees, the primary tree species of the parkland, reportedly have shallow root systems (Judd 1920), which may be injured by the trampling actions of cattle (Cline et al. 1939). Besides direct physical damage to koa root systems, cattle may be indirectly responsible for the death of trees through the removal of undergrowth, which functioned as protective cover for shallow or surface roots (Giffard 1918; Rock 1913). Another possible indirect, but detrimental, effect of cattle on koa is the compaction of soil around trees. This phenomenon, reported by Scowcroft (1971), apparently causes a reduction in pore space and thus slows infiltration rates. Compaction of soils by cattle hooves was not

indicated by the results of the present study because ranch soils had lower bulk density values than Park soils. However, soil sampling in this study was carried out in grasslands, and soils beneath the few koa trees remaining in the ranch were not sampled. Although the results af aerial photograph analysis did indicate that cattle were responsible for suppression of koa in the parkland, the question of whether the structural degradation in the parkland was due to trampling or prevention of tree regeneration is beyond the scope of this study. As previously noted, koa seedlings or suckers were not observed in the ranch, even though old, but living, koa remain in the grazed area of Keauhou. These observations, coupled with the fact that compaction was not noted in ranch sites during the present study, lend credence to the hypothesis that cattle have altered vegetation structure in the parkland by reducing tree regeneration.

In contrast to the biotic factor of introduced herbivores, fire originating from lightning or lava flows seems to be a natural perturbation in the mountain parkland (Mueller-Dombois 1967; Vogl 1969). Koa is apparently fire adapted (Vogl 1969), as thousands of koa seedlings have been observed subsequent to the occurrence of fires in koa forests (Lamoureux 1971). Seemingly, the grassland vegetation of the parkland is not permanently damaged by fire if the disturbance does not occur too frequently (Mueller-Dombois 1976). Nevertheless, fires may be more severe in Park grasslands than in those of the ranch due to the greater biomass in Park communities, as evidenced by the taller height of native bunchgrasses and shrubs. The area along the Strip Road in the Park still shows the marks of a fire which swept through the area in 1975, although little evidence of the conflagration remains in the ranch grasslands which were burned. It may be that the balance of plant composition existing in a native ecosystem merely requires a longer period of recovery time.

Floristic Composition

The grasslands of the mountain parkland are relatively simple communities composed of about 10 herbaceous species with appreciable cover (Mueller-Dombois 1975). The grass communities of the ranch are composed almost exclusively of introduced plant species. By contrast, the park grass communities are made up of both indigenous and exotic species, with the endemic grass Deschampsia australis the clear dominant in most areas.

The success of introduced grasses in the ranch portion of the study may be due to some aspect of their reproductive capacity or growth form. A decumbent growth form and production of rhizomes is often related to the ability of a grass to withstand grazing (Hanson & Churchill 1961). Two stoloniferous species almost ubiquitous in the ranch but found in none of the Park relevēs are carpetgrass and Kikuyu grass. These two grasses typically form dense mats and are able to withstand heavy

grazing because of their growth form (Whitney, Hosaka, & Ripperton 1964). Because of its extensive underground stems, Kikuyu grass is particularly adapted to undergo heavy trampling as well as grazing (Hosaka 1958). Two other grasses with a creeping or prostrate habit, which are found almost exclusively in ranch relevēs, are Bermuda grass and Brown's love grass.

Other grasses of importance in the ranch owe their success to their relative unpalatability to cattle. African dropseed and sweet vernal grass are both avoided by cattle when other forage is available. Unpalatability and the ability to reseed readily enable these two grasses to dominate some ranches (Whitney, Hosaka, & Ripperton 1964). Carpetgrass is also unpalatable to cattle (Hosaka 1957) and has a stoloniferous growth form which allows it to survive even heavy grazing. Allan (1936) reported that lovegrass and African dropseed have become established in cattle disturbed grasslands of New Zealand. They are capable of suppressing indigenous species in grazed or burned areas but have apparently not been successful in invading undisturbed indigenous communities in New Zealand. These findings support the results of this study as these same two grass species are practically non-existent in Park relevēs.

One native plant common in both ranch and Park relevēs is bracken fern, which is certainly unpalatable to cattle and may even be poisonous (Hosaka & Thistle 1954). Elsewhere in the world, ferns of this species are acutely toxic to domestic animals (Lewis & Elvin-Lewis 1977). However, other plants indigenous to the mountain parkland lack any deterrent to grazing. The grass Deschampsia is apparently palatable to cattle (Whitney, Hosaka, & Ripperton 1964), and consequently it is rarely present in ranch grassland except in rocky or shrubby areas. The endemic Mountain pili, a very palatable grass (Whitney, Hosaka, & Ripperton 1964), was not observed at all in ranch relevēs. Both these grasses are important components of the Park grasslands.

Introduced velvetgrass, generally considered a good pasture grass with acceptable palatability, occurred very infrequently in the ranch, despite being ubiquitous in the Park. The ubiquity of this grass in the Park portion of the ecosystem is promoted by pig disturbance in the mountain parkland (Spatz & Mueller-Dombois 1975). Regardless of origin, species that are preferred by cattle for forage have been eliminated and replaced by those species better adapted to withstand the pressures of grazing. Naturally, continued removal of palatable grasses allows better growth of remaining plants which are referred to as "increasers" by some authors (Weaver 1968).

This replacement of dominant native species by introduced grasses may be an indication of destructive overgrazing (Clements 1949). As has often been the case in the prairie of the Mid-West (Weaver 1963), the normal cover of the mountain parkland cannot be maintained in a range where cattle are limited in grazing

area. Spatz (1973) reported that the portion of Keauhou Ranch dominated by African dropseed, carpet grass, and Australian watergrass showed evidence of degradation. These dropseed communities were apparently indicative of drier conditions; wetter pastures near the Park boundary were dominated by Kikuyu grass. Although Kikuyu grass communities were productive, with more than twice the yield of crude protein of the dropseed communities, Spatz reported that they were heavily grazed and likely to decrease in productivity in the future in the absence of better management practices.

Fagerlund (1947) believed that a discontinuation of cattle grazing as well as a reduction in the numbers of goats and pigs would result in a decrease in the abundance of exotic plants in the Mauna Loa section of the Hawaii Volcanoes National Park. He contended that over half of the vascular plant species found in this area were exotics, and recorded 43 exotic plant species from the mountain parkland alone. It is doubtful whether any exotic species has been totally eliminated from the parkland in the past 30 years. Fagerlund's prediction that exotics would decrease in the absence of cattle grazing is not borne out by the results of this study. A number of exotics remain in the Park, despite the cessation of cattle grazing. Some of these exotics, such as velvetgrass and Australian watergrass, maintain a respectable amount of cover in the Park. Others, such as hairy catsear and sheep sorrel, may be present in small quantities but are widespread throughout the parkland ecosystem. The two latter species are of common occurrence in disturbed communities of New Zealand, but ostensibly do not aggressively displace indigenous plant species there (Allan 1936).

Velvetgrass was the second most prevalent plant species in Park grassland communities, with an average cover amounting to over 16% in study relevēs. Only the dominant endemic grass Deschampsia had a greater average cover in these releves (27%). Velvetgrass maintains this high degree of cover in the Park portion of the mountain parkland through the agency of pig digging (Spatz & Mueller-Dombois 1975). Evidence of pig digging was frequently observed during fieldwork for this study. In their search for the rhizomes of bracken and the roots and leaves of hairy catsear (Jacobi 1976; Giffin 1977), pigs expose much soil and uproot bunchgrasses. Spatz and Mueller-Dombois (1975) concluded that Deschampsia would be capable of becoming (or remaining) dominant over velvetgrass on a long-term basis if the disturbing influence of feral pigs were removed.

Even though exotics compose a sizable portion of the vegetation cover of this ecosystem in the Park, indigenous or endemic plants still constitute the bulk of the cover of the Park study segment, with more than double the cover of exotics. It is possible, of course, that exotic plant cover may have diminished in the Park in the 30 year hiatus in cattle grazing. African dropseed, the ranch dominant, was present in very small smounts in a couple of Park relevēs. It is conceivable that this grass

and other exotics were formerly more abundant in the grazed Mauna Loa strip, but this supposition is impossible to refute or affirm, lacking quantitative values for these species previous to the cessation of cattle grazing in the Park.

During the course of this study, a few small plots enclosed by Spatz (1973) on Keauhou Ranch pastures were examined, but no striking differences in species composition were observed. Evidently three years is not sufficient time for change to occur on such small (2 m X 2 m) exclosures. In New Zealand, Cockayne (1928) put a time scale of 100 years on the recovery of native rain forest which had been degraded by animals to pasture. The optimistic viewpoint of Allan (1935) and Egler (1942), regarding the potential for victory of indigenes over exotic plants, might be realized in the mountain parkland if the ecosystem were given protection from grazing for a sufficient length of time.

Clustering Tendencies of Relevēs

The classification techniques employed in this study readily separated the sample stands of the Park from those of the ranch. The synthesis table technique established one species group to represent the ranch and a different species group for Park. The four character species of Group 2 were practically ubiquitous in the ranch. In fact, the synthesis table showed a certain homogeneity among relevēs within this half of the study area. Floristic differences between sample stands were not great enough to produce species groups differentiating between the 23 relevēs located on the ranch. This was not the case with a study of Keauhou Ranch vegetation by Spatz (1973). In the area bordering the Park strip, Spatz defined at least three different groups of plant communities which he named after the dominant grass species: Pennisetum communities, Sporobolus communities, and Anthoxanthum-Axonopus communities. Within these communities he was able to establish differential species separating his relevēs into groups representing humid, dry, or exhausted conditions. The study by Spatz was an analysis of the pastures of Keauhou Ranch which encompassed a very large area and contained diverse habitats. Also, the study was based on numerous very small (2 m X 2 m) releves. These facts, coupled with the obvious exclusion of any Park communities from his sampling sites, accounts for the divergence of his results from those of this study. Three of the grasses considered dominants in Spatz's study appear as differential species in Group 2 of the synthesis tables presented here.

The species of Group 1 in the present study also appear as diagnostic species for the parkland ecosystem in two other studies. Newell (1968), in a vegetation analysis of the entire Hawaii Volcanoes National Park, found velvetgrass (along with koa) to be a differential species of the alliance encompassing the mountain parkland ecosystem. She further listed mountain pili as a differential species of the Panicum-Rumex association

within the alliance. In the present study only the grass and shrub community relevēs were used for synthesis table generation. Therefore koa could not be among the diagnostic species of the table presented, although the species is undoubtedly one of the most important of the ecosystem. Sheep sorrel, an introduced forb, was found at many of the sites of this study, but was distributed throughout both Park and ranch portions. Thus it was not a likely candidate for a character species.

In an analysis of the International Biological Program (IBP) Mauna Loa transect, Mueller-Dombois and Bridges (1975) presented a synthesis table including species groups similar to those of the present study. In the portion of the transect encompassing the mountain parkland, two species groups were important. One of these included velvet grass, Carex wahuensis, koa, pukiawe, and mountain pili. A comparison of this list with the species groups of Table 4 reveals that two out of three differential species of the Park portion of the present study were included in this species group of Mueller-Dombois and Bridges. The other two plants in their group are certainly important species, but were excluded as differential species in the present study. As only grass and shrub communities were involved in the synthesis table generation, koa appeared only rarely in the relevēs. The distribution of pukiawe in both ranch and Park portions of this study precluded it as a character species of either area. Mountain pili did not emerge as a differential species in Table 4, but the use of another set of rules produced a table (Appendix II) that did include this endemic grass in a diagnostic species group.

The third species characteristic of Park relevēs in the present study, Deschampsia, occurred in a second species group of Mueller-Dombois and Bridges. This group, including bracken fern and the shrub a'ali'i, incorporated a large number of relevēs along the Mauna Loa transect. Its distribution extended beyond the parkland ecosystem into the savanna at lower elevations and into the subalpine zone at higher altitudes. In the synthesis table presented here, it may be seen that bracken was distributed throughout both Park and ranch relevēs while a'ali'i appeared only in the Park.

The synthesis table provided an objective structure with the potential to disclose plant species which may distinguish a portion of the vegetation from the whole, thus classifying it. The use of dendrographs, also classificatory in nature, permitted the graphic display of the relationships between sample stands.

The clustering tendencies revealed by the dendrographs indicated a dichotomy of Park and ranch areas, substantiating the similar outcome of the synthesis table. The second dendrograph is to be preferred, for the reason that it utilized the quantitative data which were available. This method also tends to confirm the previous interpretations of the vegetation based on the floristic composition of the two areas. All techniques

employed to analyze the mountain parkland vegetation support the hypothesis that grazing has greatly altered the ranch portion of this ecosystem.

In addition, the dendrograph based on presence-absence data upholds the second hypothesis of this study, that cattle grazing has suppressed variation along the altitudinal gradient in the mountain parkland. Acceptance of this hypothesis is encouraged by the existence of clusters of Park relevēs in the dendrograph which are separated on the basis of their elevational position. The critical elevation where this separation occurs is near the mid-point of the study area between 5200 and 5400 feet. Park grassland relevēs exhibited altitudinal variation, whereas the ranch grassland relevēs were more uniform. This study provides evidence that, through grazing, cattle are capable of suppressing the natural effects of altitude on vegetation variation.

Soils

While many of the differences in the vegetation of the grazed and ungrazed portions of the parkland ecosystem were obvious, the effects of grazing on the soils of the area were more subtle and less visible. The differing soil depths of the two areas were probably not attributable to any detrimental effects of cattle upon the ranch. No evidence of serious erosion was discovered on the ranch portion of the study area, but past ranch practices included the clearing of shrubs, which may have resulted in loss of soil (Apple 1954). Another possible explanation for shallower ranch soils may be found in the nature of the origin of the soil parent material. The parkland soils are derived from variable ash deposits (Doty & Mueller-Dombois 1966); therefore, the variation in soil depth of the ranch and Park sites may be due to the differences in depth of the ash layer inherent in the region.

At least two other authors have reported variable soil depths for the mountain parkland. Spatz (1973) listed soil depths in Sporobolus communities of Keauhou Ranch ranging from 12 to 100 cm. The soil depths reported by Rajput (1968) for grass and shrub communities in the mountain parkland segment of the Hawaii Volcanoes National Park ranged from 14 to 50 cm, and were similar to the mean depths of the Park relevēs in the present study.

The results from the investigation of the bulk density of parkland soils were inconclusive. Other authors have reported that grazing increased the bulk density of surface soils by compaction (Duvall & Linnartz 1972; McCarty & Mazurak 1976). Adams (1975) cited a study in which grazing increased the bulk density of a woodland soil by 29%. Another study (Linnartz et al. 1966) reported increases in the bulk density of Louisiana woodland soils ranging from 1 to 7%, according to the soil horizon and the intensity of grazing. The results of the present

study showed that the bulk density values of ungrazed Park soils were greater than those of the ranch soils which supported grazing. This circumstance is not without precedent, as Yamamoto (1963) reported that mean bulk density was higher for soils of "idle" grassland than for pastureland soils.

The mountain parkland soils had bulk densities ranging from 0.48 to 1.00 g/cm , values about half as large as would be expected for North American soils with a sandy loam texture (Buckman & Brady 1969). These densities are not exceptional for Hawaiian soils, which are known to have relatively low volume weights (Moir et al. 1936). Values obtained during the present study are also somewhat higher than the bulk density of 0.54 g/cm reported for a Hanipoe series soil in an upland forest of Hawai'i within the elevation belt of the parkland ecosystem. Parkland soil bulk densities correspond quite well to bulk density determinations for many soil series of the Island of Hawai'i listed by Sato et al. (1973). As the bulk density values were relatively low, it may be stated that none of the soils examined were compacted. The observed disparity in bulk density values of Park and ranch soils may not be attributed to the effects of cattle, and is possibly an indication of the unreliability of any conclusion based on a paucity of sample cores.

The results of soil moisture constant determinations in the mountain parkland were unexpected, as ranch soils were found to retain more moisture than Park soils at both field capacity and permanent wilting point. These constants are based on soil texture and structure, and the soils examined appeared to fall in much the same textural class. Soil structures were not investigated, so it it possible that they differ in the two areas. Although the soils of both Park and ranch had similar amounts of pore space, the size of these pores may vary in the two segments of the study. Linnartz et al. (1966) noted that grazing did not alter texture, moisture constants, or particle density of Louisiana forest soils.

Ranch soil moisture retention at both pressure approximations compared very favorably with the soil moisture contents determined for Hawaiian pastureland soils by Yamamoto (1963). In the same study, Yamamoto presented mean values for moisture constants from "idle" grasslands in Hawai'i that were considerably higher than the soil moisture retention results obtained for Park soils in the present study. Water content at field capacity and permanent wilting point for Apakuie soils, determined by Sato et al. (1973), was found to be much higher than the values of percentage moisture under pressure approximations for most soils in the present study, but was similar to extreme values observed for parkland soils.

In the present study the percentage available moisture or storage capacity of A horizon soils was much the same for Park and ranch relevés, being 16.8 and 16% respectively. Actual soil moisture data were not collected in this study, but some figures

are available for parkland soils. Myers (1974) reported soil moistures of 20.2%, 31.7%, and 32.1% for three sites along the Mauna Loa Strip Road where vegetation cover consisted of koa trees and grasses. Stoner et al. (1975) found that soil moisture in the mountain parkland ranged from 18 to 27%. In Alberta, Canada, Johnston (1962) found that the water-intake rate and percentage soil moisture decreased as the intensity of grazing increased. Other authors have reported that grazing has the effect of lowering the percentage moisture of soils (Ellison 1960; Beebe & Hoffman 1968; Johnston et al. 1971). On the basis of Park vegetation structure, Park soils might be expected to contain more moisture than ranch soils. The number of trees in the Park is much greater than in the ranch, and these trees are undoubtedly effective in intercepting cloud or fog drip, which is reported to be an important component of total precipitation in the ecosystem (Juvik & Perreira 1973).

The pH values for parkland soils ranged from slightly to moderately acid, with the ranch soils being more acidic than those of the Park. Spatz (1973) reported pH values for Keauhou Ranch soils that compare well with the data collected in the present study. pH values for Park soils in the mountain parkland reported by other authors (Rajput 1968; Myers 1974; Stoner et al. 1975) range from 5.0 to 6.5 and substantiate the higher pH values of Park soils in this study. The observed differences in soil pH for the two areas may be related to the very different vegetation cover of the two areas, an indirect effect of grazing.

Some authors have reported that grazing tends to raise the pH of soils (Beebe & Hoffman 1968; Johnston et al. 1971), while the opposite effect has also been attributed to grazing (Smoliak et al. 1972). In the latter case, increased organic matter was the factor that may have stimulated the pH reduction under a regime of grazing. Decomposition of organic matter in the soil tends to reduce the pH toward the acid end of the scale (McCall 1973). Spatz (1973) noted a positive correlation between soil acidity and increased organic matter in Keauhou Ranch. Higher levels of organic carbon in ranch soils are implicated as an important factor relating to the lower pH values noticed in ranch soils of the present study.

Results from nutrient analyses of Park and ranch soils indicated that the ranch has not engaged in soil fertilization in the recent past, or at least that any such efforts have had little effect on the levels of four important macro-nutrients. Phosphorus occurred at very low levels in the present study, this is one nutrient commonly deficient in Hawaiian pastures (Younge & Otagaki 1958; Plucknett 1970). The ranch's failure to fertilize is surprising, as treatment with nitrogen-phosphorus-potassium fertilizer has been shown to increase the carrying capacity and beef production of Pennisetum (Kikuyu grass) pastures in Hawaii (Tamimi et al. 1968). Spatz (1973) calculated that several of the grass communities of Keauhou Ranch could yield double the amount of protein, and therefore result in double the beef production, if the soil were fertilized.

Leaf (1958) reported decreases of phosphorus, potassium, calcium, and magnesium in forest soils which he attributed to the removal of forage by cattle. Other writers have presented results indicating that grazing is responsible for reduction in levels of calcium and sodium (Smoliak et al. 1972), as well as phosphorus (Johnston et al. 1971). As fertility levels in the Park and ranch soils were so similar no such influence of grazing was noted in this study.

Organic carbon values for surface soils of Park relevés were considerably lower than percentage carbon values from the mountain parkland presented by others (Stoner et al. 1975). Myers (1974) listed percentage organic matter values from soils collected under koa trees ranging from 18.1 to 26.4% (10.5 to 15.3% organic carbon). Rajput (1968) presented figures for percentage organic carbon from parkland soils ranging from 2.91 to 15.8%. Most of his sites appeared to incorporate koa colonies; tree litter may account for the higher organic carbon values recorded. The community in which the lowest value occurred was described by Rajput as a grassy matrix community with scattered shrubs. Figures for percentage organic carbon in soils of Kipuka Ki and Kipuka Puaulu (both forest and savanna) below the parkland ecosystem were also higher than those of the Park soils presented in this study (Mueller-Dombois & Lamoureux 1967). Sato et al. (1973) listed organic carbon determinations for Apakuie series soils which were almost double those of ranch soils and three times as large as the organic carbon values of Park soils. Nevertheless, the organic carbon values for these Park soils do compare favorably with those reported from other tropical grasslands (Mueller-Dombois & Perera 1971) and grasslands in the Hawaiian Islands (Yamamoto 1963).

There was great variability in the values of organic carbon in soils examined during this study, and several rather extreme values were recorded. Several possible explanations for this phenomenon exist. First, the Walkley-Black method of organic carbon analysis is thought to give variable results, although it is a widely used soil test due to the rapidity with which it may be carried out (Walkley 1947). Second, the range of variability for organic matter in Hawaiian soils is reportedly large (McCall 1973). Third, the churning and overturning of soils in the Park, which is the consequence of feral pig digging activity, may be responsible for mixing horizons, bringing less rich soil to the surface, and thus lowering organic matter in disturbed patches.

One of the most confusing results of this study is the higher organic carbon values in ranch soils. The decrease of organic carbon or organic matter in soils under a regime of grazing has been reported by several authors (Leaf 1958; Beebe & Hoffman 1958). Johnston et al. (1971) gave increased erosion as well as mulch and forage removal as causes for reduced organic matter in Canadian soils. Weaver and Rowland (1952) found that protection of a native prairie in Nebraska resulted in a 2% increase in the organic matter of surface soils. The opposite

case, where percentage carbon (as well as C/N ratio) increased under grazing, may be found in a study of Canadian prairies grazed by sheep (Smoliak et al. 1972). This increase in organic carbon was attributed to sheep manure deposits and a change in species composition which increased the amount of shallow roots in the grazed soil. In a later study, the authors (Dormaar et al. 1977) confirmed these findings of increased organic carbon with grazing. Yamamoto (1963) presented data from Hawaiian soils indicating that organic matter was somewhat higher in pastureland (grazed) soils than in soils of ungrazed or "idle" grasslands.

Dean et al. (1975) calculated that 43% of the gross energy consumed by cattle on a short-grass prairie was returned to the soil in the form of faecal material. Their conclusion was that the major impact of the grazing animals was the diversion of above-ground biomass from the litter component. In the present study, there appeared to be little diversion from the litter component of the ranch relevés, since litter cover was higher there than in the Park relevés. It is possible, though, that organic material returned to the soil in faecal material is more readily broken down and incorporated into the soil. Also the deposition of feces may serve to localize this organic matter, and chance may account for the higher values recorded for ranch relevés.

Organic carbon was the key soil property of this study which could be correlated to other soil results. Higher ranch values for this property influenced the lower bulk density and higher moisture retention properties, as well as the increased acidity observed in ranch soils. A number of factors may be considered in order to attempt identification of the underlying cause of this ranch organic carbon accumulation.

The differing composition of plant species in the two areas may covertly influence the soil organic matter. Decomposition rates of plant litter may be different in two areas where the plants that constitute the litter differ (Vogl 1969; Williams & Gray 1974). The ranch grasses might conceivably be less resistant to decomposition and release more organic matter to the soil. The different grass species of Park and ranch may vary as to the amount of nitrogen in their tissues. More soil organic matter would result from the decomposition of plants with tissues high in nitrogen (McCall 1973). Along the same line, Weaver and Rowland (1952) reported that plant species in their prairie study differed in their ability to enrich the soil. Concerning the mountain parkland, it is conceivable that nutrient cycling is such that in the Park a greater percentage of the organic matter of the ecosystem is bound within the living plant tissue, as the Park surely has a greater biomass than the ranch.

The differing root distributions of unlike grass species may influence the amount of organic matter in soils. Smoliak et al. (1972) proposed that the dense, shallow roots of grass species made prevalent by sheep grazing were the cause of increased soil

organic carbon in ranch soils. Daubenmire and Colwell (1942) presented much the same explanation for higher observed organic matter for soils under a regime of grazing.

Another possibility for this disparity may involve a difference in microbiological activity in the ranch and Park. Soils of the ranch were more acid, which could have stimulated fungal activity (Stoner et al. 1975) and led to higher amounts of organic matter entering soil from the litter layer. Acid soils may accumulate organic matter by slowing its further decomposition (Etherington 1975).

As fog interception is thought to be an important component of parkland precipitation, the dearth of trees in the ranch may lessen the moisture entering the soils there. As the parkland climate is seasonal with dry summers, the lack of additional moisture from fog interception during dry periods may cause ranch soil moisture to be more seasonally variable than that of Park soils. This factor may contribute to a lessened degree of leaching of organic matter from the soils, provided that moisture is not so limited as to impair the fungal activity of litter decomposition. Also, the further decomposition of organic matter may be seasonally disrupted in ranch soils, while being continuous in Park soils with their more uniform moisture content. Another possibility is that types of fungal species with disparate rates of organic matter utilization may characterize the soils of park and ranch. Most of these ideas are of a conjectural nature and are unsupportable in the framework of the present study.

CONCLUSIONS

This study has detailed the effects of cattle on the vegetation and soils of the mountain parkland ecosystem, completing the preliminary investigations of the impact of introduced mammals on the vegetation of the ecosystem. Each technique utilized to evaluate the vegetation of this ecosystem led to the conclusion that cattle grazing was responsible for the alteration of the structure and floristic composition of the mountain parkland. In addition, the graphic method of cluster analysis by dendrograph supported the second hypothesis regarding the suppression of altitudinal variation in vegetation by cattle. The soil results were not entirely as expected and did not substantiate the third hypothesis that cattle grazing had detrimental effects on parkland soils. The failure of the results of this study to validate this third hypothesis may be a function of the time factor involved. After more than a century of grazing, vegetation of the parkland appears to have been more readily affected by the presence of cattle than have soils. Since the soil underlying the altered vegetation of the ranch

portion of this study showed no real deterioration, there is always the possibility that the natural parkland vegetation may become re-established in the future.

The mountain parkland is a small but distinct ecosystem along the Mauna Loa transect, representing a type of vegetation formerly more widespread, but presently much reduced on the island of Hawai'i. When this area was incorporated into Hawaii Volcanoes National Park, it was valued not as a remnant of a disappearing vegetation, but merely as an access to the Mauna Loa summit from the larger Kilauea section of the Park (Apple 1954). It is unfortunate that a larger segment of this ecosystem was not set aside 50 years ago, for in its present limited condition the mountain parkland is more vulnerable to man-made disturbances such as the fire which burned over a thousand acres of koa studded grassland in August 1975. Nevertheless, if such disturbances are infrequent, the mountain parkland of Mauna Loa will remain an important remnant of a disappearing Hawaiian ecosystem.

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TABLE 1. Origin of grass species found in relevēs

Species	Present in Park	Present in Ranch	Region of Origin	Date of Arrival or Collection
Andropogon virginicus	x		North and Central America	1932
Anthoxanthum odoratum	x	x	Eurasia	1906
Axonopus affinis		x	Tropical America and South U.S.	1912
Bromus rigidus	x		Europe	1906
Cynodon dactylon		x	Old World	1835
Deschampsia australis	x	x	Hawaiian Islands	endemic
Eragrostis brownei	x	x	Australia	1906
Holcus lanatus	x	x	Europe	1906
Panicum tenuifolium	x		Hawaiian Islands	endemic
Paspalum dilatatum	x	x	South America	1906
Pennisetum clandestinum		x	Tropical Africa	1924
Sporobolus africanus	x	x	South Africa	1906

(Whitney, Hosaka, and Ripperton 1964)

TABLE 2. Percentage cover of exotic and indigenous plants in study relevēs

Site and Relevē No.	Park Exotic	Park Indigenous	Site and Relevē No.	Ranch Exotic	Ranch Indigenous
1P1	51.2	17.6	1R4	69.2	0
1P2	50.8	21.6	1R5	66.8	0
2P1	43.6	26.4	2R4	54.0	7.6
2P2	39.2	32.4	2R5	52.8	4.0
2P3	1.6	84.8	2R6	36.0	36.0
3P1	35.6	27.2	3R4	50.4	2.0
3P2	66.0	8.0	3R5	50.8	1.2
3P3	9.2	63.2	3R6	11.2	62.8
4P1	25.2	38.8	4R4	54.8	5.2
4P2	32.0	32.4	4R5	49.6	6.0
4P3	6.8	82.0	4R6	28.0	36.4
5P1	17.2	42.4	5R4	59.6	0.4
5P2	15.2	46.8	5R5	54.4	2.0
5P3	12.0	76.0	5R6	28.8	51.2
6P1	27.2	37.2	6R4	32.8	22.4
6P2	37.2	20.8	6R5	41.2	11.6
6P3	6.4	70.0	6R6	11.2	65.6
7P1	5.2	75.6	7R4	71.2	0
7P2	2.4	66.0	7R5	76.8	0
7P3	10.8	69.6	7R6	21.6	48.4
8P1	14.8	38.8	8R4	56.8	0
8P2	20.4	51.2	8R5	68.0	0
8P3	6.0	62.8	8R6	21.6	56.0

TABLE 3. Braun-Blanquet cover abundance scale

Value	Cover
1	Numerous but less than 5% cover
2	5-25% cover
3	25-50% cover
4	50-75% cover
5	More than 75% cover
6(+)	Few with small cover
7(r)	Solitary with small cover

TABLE 4. Two-way synthesis table of parkland cover data made with 66/33 threshold values

Site	1P	2P	2P	2P	3P	3P	3P	4P	4P	4P	5P	5P	5P	6P	6P	6P	7P	7P	7P	8P	8P	8P	1R	1R	2R	2R	2R	3R	3R	3R	4R	4R	5R	5R	5R	6R	6R	7R	7R	7R	8R	8R	8R	1P	4R	6R
Relevé	2	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	4	5	4	5	6	4	5	6	4	5	4	5	6	4	5	4	5	6	4	5	6	1	6	6
Species Group 1																																														
Species	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*																								
Deschampsia australis	2	2	2	1	2	1	2	3	3	2	3	3	2	3	2	2	4	4	2	3	3	2					1			2					1	2	2								1	2
Holcus lanatus	3	2	2	1	2	3	2	2	2	1	1	1	2	2	3	1	1	6	2	2	2	1	6		6													6					2		
Carex wahuensis		1	1	6	1			1	6	6	6	2	6	6	6	6	1	6	6	6	2																								
	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*																								
Species Group 2																							*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*
Sporobolus africanus		6	6																				2	2	3	3	2	2	3	2	3	3	3	2	2	2	2	3	3	2	2	1	1		2	
Cattle feces																							6	1	1	1	6	6	1	6	1	2	1	1	1	6	6	1	1	6	1	1	6		6	6
Axonopus affinis																							6	1	2	1	2	2	2	1	2	2	6	2	1	1	1	2	2	6	2	6	6		2	
Eragrostis brownei																				6					6		6	6	6	6				1	6	2	2	6	6	2	1	2	2			
Pennisetum clandestinum																							3	3	6	1		1	1		2	2	3	2	1			2	2	6	6	3				
																							*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*			
Litter	3	2	2	2	2	3	2	3	3	2	3	3	2	2	3	2	2	3	2	2	2	2	3	3	3	3	2	3	3	2	3	3	3	3	2	3	3	2	2	2	3	3	2	2	2	2
Hypochoeris radicata	5	1	1	6	1	6	5	1	1	1	1	6	6	1	5	1	1	1	1	1	2	1	1	6	1	1	1	1	1	1	1			6	1	6	1	6	6	2	6	1	1	6	6	6
Anthoxanthum odoratum	1	2	2	6	2	1	6	1	2	6	2	2	2	2	1	6			6		6		2	2	2	2	2	2	2	1	2	1	2	2	1	2	2	2	2	1	2	2	2	6	1	2
Bare soil	6	2	2	1	2		1	2	1	1	1	2	1	2	2	1	1	1	1	2	2	2			1	1	2	2	2	1		1		1	1	2	2	1	6	1	1	6	2		2	2

TABLE 4. (Continued) Two-way synthesis table of parkland cover data made with 66/33 threshold values

Site	1	2	2	2	3	3	3	4	4	4	5	5	5	6	6	6	7	7	7	8	8	8	1	1	2	2	2	3	3	3	4	4	5	5	5	6	6	7	7	7	8	8	8	1	4	6
Relevé	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	P	R	R
	2	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	4	5	4	5	6	4	5	6	4	5	4	5	6	4	5	4	5	6	4	5	6	1	6	6
Species																																														
Exposed rock		6	1	6	1		6	1	6	6	1	1	1	1	2	1	6	6	1	2	1	2			6	1	2	1	2	1	6	1		1	1	1	1		1	1	6	6	2		1	1
Pteridium aquilinum	2	2	2	1	2	1	1	2	1	1	1	3	6	1		1					6	6	6	6	2	1	1	1	6	1	2	2	6	1	1	6	1						2	1	6
Styphelia tameiameiae		1	1	3		6	3			4	3		4	3		3			4		2	3			1		3	6	6	4		6			3					2			3		3	3
Rumex acetosella	6	6	6		6	1		6	6						6								6		6	1	6	6	6		6	6			6		6		6						
Paspalum dilatatum	2	2	1	6	1	3	2		6							6							6				6		6						6			1	1	6			1	2		
Panicum tenuifolium		6	1		1			1	1			1	1	6	6				1	6	2	6																								
Carex macloviana						6			6		1			6	6																													6			
Lotus angustissimus																							6								6						6	6		1				6	
Vaccinium reticulatum																					1	2																	3		6	2					
Plantago lanceolata						6	6	6																				6																	
Bodonaea sandwicensis		6		3			1														6																								
Dead wood											2								1															6	6										
Andropogon virginicus					7							7																	7																	
Cirsium vulgare									7						7																								7						

TABLE 4. (Continued) Two-way synthesis table of parkland cover data made with 66/33 threshold values

Site	1	2	2	2	3	3	3	4	4	4	5	5	5	6	6	6	7	7	7	8	8	8	1	1	2	2	2	3	3	3	4	4	5	5	5	6	6	7	7	7	8	8	8	1	4	6
	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R
Relevé	2	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3	4	5	4	5	6	4	5	6	4	5	4	5	6	4	5	4.	5	6	4	5	6	1	6	6
Species																																														
Cynodon dactylon																															6		6					6								
Coprosma ernodeoides										2																													6			6				
Acacia koa				7													7																													
Medicago sp.																																								6	6					
Veronica plebeia																																	6	6											
Epilobium cinereum					1																																								
Centaurium umbellatum																													6																
Tree root													7																																
Rhacomitrium sp.																	6																												
Usnea sp.																	7																												
Goat droppings																						6																						
Bromus rigidus																																											7		
Juncus tenuis																																									7				
Fragaria vesca																																										6			

TABLE 5. Soil types of study sites

Site	Elevation	Soil Type	
		Park	Ranch
1	4600'	HDD	HDD
2	4800'	HDD	HDD
3	5000'	HDD	HCD
4	5200'	HDD	HCD
5	5400'	HCD	HCD
6	5600'	ASD	ASD
7	5800'	ASD	HCD
8	6000'	ASD	HCD

HDD = Hanipoe Soil Series, silt loam

HCD = Hanipoe Soil Series, very stony loam

ASD = Apakuie Soil Series, very stony, very fine sandy loam (Sato et al. 1973)

TABLE 6. Textural classification of A horizon soils at selected sites

Site	Elevation	Park				Ranch			
		Sand	Silt	Clay	Class	Sand	Silt	Clay	Class
1	4600'	53%	35%	12%	loam	59%	33%	8%	sandy loam
5	5400'	52%	39%	9%	sandy loam	53%	40%	7%	sandy loam
8	6000'	51%	39%	10%	loam	49%	43%	8%	sandy loam

TABLE 7. Porosity or percentage total pore space of soils

Site	Elevation	Park	Ranch
1	4600'	74%	74%
2	4800'	62%	69%
3	5000'	71%	78%
4	5200'	67%	75%
5	5400'	72%	74%
6	5600'	77%	75%
7	5800'	72%	82%
8	6000'	70%	80%

TABLE 8. Correlation coefficients (r) between percentage organic carbon and other soil properties

	Organic Carbon A Horizon	Organic Carbon B Horizon
pH	-0.68	-0.73
Bulk density	-0.79	---
Field capacity	+0.82	+0.44
Permanent wilting percentage	+0.89	+0.56

TABLE 9. Percentage cover of species in grass community relevés

Species	Site Number and Location 1		2		3		4		5		6		7		8	
	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch
Deschampsia australis (E)	8.0		13.8		9.4		25.6		35.8		24.4	15.8	68.4		33.0	
Holcus lanatus (X)	22.2	+	20.8	0.4	23.6		19.0		3.8		26.4		4.0	0.4	12.2	
Panicum tenuifolium (E)			1.8		2.0		2.4		4.4		0.6				3.0	
Carex wahuensis (E)			1.2		2.8		1.2		3.4		0.4		3.6		4.6	
Carex macloviana (I)	+				0.4		0.8		1.2		0.6					
Sporobolus africanus (X)		12.6	0.4	33.2		24.0		28.8		23.0		14.6		34.4		12.0
Axonopus affinis (X)		1.4		6.0		11.4		10.6		8.8		2.8		8.8		7.2
Pennisetum clandestinum (X)		43.2		2.8		1.4		7.0		20.8				12.4		30.8
Eragrostis brownei (X)				0.4		0.4				1.6		6.8		0.6	0.4	3.8
Cattle feces		1.0		3.4		1.6		4.8		4.4		0.8		2.4		2.6
Anthoxanthum odoratum (X)	1.2	10.2	9.2	9.0	8.6	9.0	6.4	4.6	11.0	6.8	3.8	11.0		15.4	+	21.4
Hypochoeris radicata (X)	+	1.2	2.0	2.4	0.8	3.6	2.4	1.2	1.2	0.4	1.8	1.6	1.8	0.4	5.2	1.4
Litter	29.2	29.0	20.6	32.4	25.0	36.6	28.6	36.0	27.0	34.8	26.2	30.8	22.8	20.8	17.2	33.6
Rock			1.4	1.0	1.2	4.4	1.4	0.8	2.0	1.6	6.2	3.6	0.6	1.2	4.0	0.4
Bare soil	0.4		7.2	3.0	12.4	6.2	5.8	1.2	5.4	2.4	6.4	10.8	2.0	1.0	14.6	1.0

TABLE 9. (Continued) Percentage cover of species in grass community relevés

Species	Site Number and Location															
	1		2		3		4		5		6		7		8	
	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch
Pteridium aquilinum (E)	15.6	+	8.8	5.0	5.4	1.4	6.0	5.6	2.0	1.2	1.2	1.2			0.4	
Rumex acetosella (X)	0.8	+	0.6	1.0	1.8	0.6	0.8	0.4			+	0.4	+			
Styphelia tameiameiae (I)			3.4	1.6	0.4	0.4		+	1.2		4.8				6.8	
Paspalum dilatatum (X)	27.8	+	8.6		15.2	0.4	0.4						1.6			
Lotus angustissimus (X)		+						0.8					0.8			1.6
Plantago lanceolata (X)					0.4	0.4	0.4									
Cynodon dactylon (X)								+		0.4			+			
Cirsium vulgare							r				0.4		r			
Andropogon virginicus (X)					r				0.4							
Dodonaea sandwicensis (E)					0.8										+	
Vaccinium reticulatum (E)															1.6	+
Dead wood									7.2						2.4	
Centaurium umbellatum (X)						+										
Veronica plebeia (X)										0.8						

TABLE 9. (Continued) Percentage cover of species in grass community relevés

Species	Site Number and Location							
	1	2	3	4	5	6	7	8
	Park Ranch	Park Ranch	Park Ranch	Park Ranch	Park Ranch	Park Ranch	Park Ranch	Park Ranch
Medicago sp. (X)								0.4
Epilobium cinereum (X)			1.2					
Juncus tenuis (X)								+
Bromus rigidus (X)	+							
Acacia koa (E)							r	
Moss							0.8	
Usnea sp.							0.4	

TABLE 10. Percentage cover of species in shrub community relevés

Species	Site Number and Location													
	2		3		4		5		6		7		8	
	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch
Holcus lanatus (X)	1.2		8.4		3.2		5.2		1.2		6.0		3.6	
Carex wahuensis (E)	0.8				0.8		0.4		0.4		0.8			
Panicum tenuifolium (E)							1.2				1.2		0.4	
Dodonaea sandwicensis (E)	47.6		4.0											
Cattle feces		0.4		+		+		1.2		0.8		0.8		+
Sporobolus africanus (X)		17.2		6.0		18.0		13.6				6.8		1.2
Axonopus affinis (X)		10.4		1.6		8.0		4.8				0.8		0.4
Eragrostis brownei (X)		+		+				+				14.4		10.0
Pennisetum clandestinum (X)								4.8				+		
Styphelia tameiameiae (I)	28.4	28.0	42.8	55.2	58.8	33.2	54.8	45.6	45.6	44.8	55.6	22.0	34.8	42.4
Hypochoeris radicata (X)	+	2.8	0.8	1.6	3.2	0.4	0.4	3.2	4.4	0.8	4.8	5.2	2.4	2.8
Litter	10.4	19.2	10.0	18.8	8.8	22.8	8.8	10.8	21.2	10.0	13.6	16.8	12.0	8.0

TABLE 10. (Continued) Percentage cover of species in shrub community relevés

Species	Site Number and Location													
	2		3		4		5		6		7		8	
	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch
Bare soil	2.4	2.8	4.0	4.0	2.0	8.0	1.6	4.0	1.2	9.2	4.8	1.2	14.0	8.4
Rock	0.8	5.6	+	3.2	0.4	4.8	1.2	4.0	1.2	3.2	1.2	2.8	5.2	6.0
Anthoxanthum odoratum (X)	0.4	5.2	+	1.6	0.4	1.6	6.0	2.0	0.8	10.0	+	2.8		5.6
Deschampsia australis (E)	4.0	4.0	11.6	5.6	11.2	1.2	19.2	1.6	22.4	20.4	12.0		9.6	
Pteridium aquilinum (E)	3.6	4.0	4.8	2.0	1.6	2.0	0.4	4.0	1.6	0.4			0.8	
Paspalum dilatatum (X)	+	0.4	13.6					+	+			+		1.6
Vaccinium reticulatum (E)												26.0	17.2	13.6
Coprosma ernodeoides (E)					9.6							0.4		+
Rumex acetosella (X)		+						0.4						
Lotus angustissimus (X)										0.4				
Fragaria vesca (X)														+
Andropogon virginicus (X)				0.4										

TABLE 10. (Continued) Percentage cover of species in shrub community relevés

Species	Site Number and Location						
	2	3	4	5	6	7	8
	Park Ranch	Park Ranch	Park Ranch	Park Ranch	Park Ranch	Park Ranch	Park Ranch
Acacia koa (E)	0.4						
Plantago lanceolata (X)		+					
Goat feces							+
Tree root				0.4			

TABLE 11. (Continued) Mean height (cm) of species in grass community relevés

Species	Site Number and Location													
	1		2		3		4		5		6		7		8	
	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch
Hypochoeris radicata		11.0	24.1	9.8	21.3	6.8	21.0	7.0	13.0	14.0	7.5	3.2	14.0	6.0	17.4	5.8
Rumex acetosella	21.0		42.0	12.8	31.4	11.0	18.0	6.0				6.0				
Lotus angustissimus								8.0								3.5
Veronica plebeia									4.0							
Plantago lanceolata							34.0									
Epilobium cinereum					35.5											
Cirsium vulgare											50.0					
Styphelia tameiameiae			60.8	29.5					40.0		45.9				54.3	
Vaccinium reticulatum															39.0	
Dodonaea sandvicensis			40.0													

TABLE 11. Mean height (cm) of species in grass community relevés

Species	Site Number and Location 1		2		3		4		5		6		7		8	
	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch
Deschampsia australis	46.6		28.1		24.6		27.2		23.1		21.7	19.3	24.6		20.7	
Panicum tenuifolium			48.7		34.3		30.8		32.4		32.5				35.8	
Holcus lanatus	41.9		26.9		26.9		23.1		14.1		39.4		20.9		14.6	
Anthoxanthum odoratum	41.3	17.0	25.5	22.0	28.2	12.8	29.1	12.6	21.9	10.3	19.0	14.1	11.2		9.1	
Sporobolus africanus		12.2	19.0	9.6		7.9		6.8		7.3		8.1	8.0		7.6	
Axonopus affinis		6.4		6.6		5.6		4.5		4.8		5.3	4.6		4.2	
Pennisetum clandestinum		5.0		2.5		2.0		4.3		3.2			2.5		2.6	
Eragrostis brownei				12.0						6.6		6.1	14.5		5.4	
Paspalum dilatatum	32.7		25.6		18.5	22.0	15.0									
Andropogon virginicus									15.0							
Carex wahuensis			19.5		15.2		21.2		11.7		19.0		20.0		16.8	
Carex macloviana							6.0		10.0		14.0					
Pteridium aquilinum	48.7		29.4	17.2	22.9	17.2	33.6	16.2	16.1	14.2	23.3	16.4			36.0	

TABLE 12. Mean height (cm) of species in shrub community relevés

Species	Site Number and Location													
	2		3		4		5		6		7		8	
	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch
Styphelia tameiameiae	102	39.0	93.4	46.0	127	38.9	117	103.3	69.9	120.3	164	49.4	57.4	56.5
Vaccinium reticulatum												35.1	36.8	35.9
Dodonaea sandwicensis	154		152											
Deschampsia australis	11.6	21.3	38.7	30.2	22.3	67.5	30.2	3.7	16.7	13.9	20.5		14.9	
Holcus lanatus	8.3		33.9		27.2		26.3		22.0		18.9		18.4	
Panicum tenuifolium							36.0				25.7		8.0	
Anthoxanthum odoratum		16.5		23.3	6.5	15.8	6.3	16.8	16.0	7.5		12.1		8.6
Sporobolus africanus		10.5		8.5		6.5		7.2				6.2		8.0
Axonopus affinis		7.7		4.0		4.2		4.0						
Eragrostis brownei												5.8		2.8
Paspalum dilatatum			29.1											3.0

TABLE 1[illegible]. (Continued) Mean height (cm) of species in shrub community relevés

Species	Site Number and Location													
	2		3		4		5		6		7		8	
	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch	Park	Ranch
Pennisetum clandestinum														
Andropogon virginicus								4.9						
Carex wahuensis			21.0											
Pteridium aquilinum	30.0								7.0		16.0			
Hypochoeris radicata	25.1	23.8	49.0	13.6	17.0	15.3		19.0	40.0				20.0	
		5.3	2.0	15.0	2.0	10.0	7.0	2.0	9.4	12.0	9.9	4.2	8.7	1.0

TABLE 13. Two-way synthesis table of parkland cover data made with 66/10 threshold values

Site	1	1	2	2	2	3	3	3	4	4	5	5	5	6	6	7	7	7	8	8	8	1	1	2	2	2	3	3	3	4	4	4	4	5	5	5	6	6	6	6	7	7	7	8	8	8
	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Relevé	4	5	4	5	6	4	5	6	4	5	4	5	6	4	5	4	5	6	4	5	6	1	2	1	2	3	1	2	3	1	2	3	6	1	2	3	1	2	3	6	1	2	3	1	2	3
Species	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*																									
Sporobolus africanus	2	2	3	3	2	2	3	2	3	3	3	2	2	2	2	3	3	2	2	1	1			6	6									2												
Cattle feces	6	1	1	1	6	6	1	6	1	2	1	1	1	6	6	1	1	6	1	1	6													6						6						
Axonopus affinis	6	1	2	1	2	2	2	1	2	2	6	2	1	1	1	2	2	6	2	6	6													2												
Eragrostis brownei			6		6	6	6	6				1	6	2	2	6	6	2	1	2	2																					6				
Pennisetum clandestinum	3	3	6	1		1	1		2	2	3	2	1			2	2	6	6	3																										
	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*																										
Litter	3	3	3	3	2	3	3	2	3	3	3	3	2	3	3	2	2	2	3	3	2	2	3	2	2	2	2	3	2	3	3	2	2	3	3	2	2	3	2	2	2	3	2	2	2	2
Hypochoeris radicata	1	6	1	1	1	1	1	1	1	·		6	1	6	1	6	6	2	6	1	1	6	6	1	1	6	1	6	6	1	1	1	6	1	6	6	1	6	1	6	1	1	1	1	2	1
Anthoxanthum odoratum	2	2	2	2	2	2	2	1	2	1	2	2	1	2	2	2	2	1	2	2	2	6	1	2	2	6	2	1	6	1	2	6	1	2	2	2	2	1	6	2			6		6	
Bare soil			1	1	2	2	2	1		1		1	1	2	2	1	6	1	1	6	2		6	2	2	1	2		1	2	1	1	2	1	2	1	2	2	1	2	1	1	1	2	2	2
Exposed rock			6	1	2	1	2	1	6	1		1	1	1	1		1	1	6	6	2			6	1	6	1		6	1	6	6	1	1	1	1	1	2	1	1	6	6	1	2	1	2
Pteridium aquilinum	6	6	2	1	1	1	6	1	2	2	6	1	1	6	1							2	2	2	2	1	2	1	1	2	1	1	1	1	1	6	6	1		1	6				6	6
Deschampsia australis					1			2					1	2	2								2	2	2	1	2	1	2	3	3	2	1	3	3	2	3	2	2	2	4	4	2	3	3	2
Holcus lanatus	6		6														6					2	3	2	2	1	2	3	2	2	2	1		1	1	2	2	3	1		1	6	2	2	2	1

TABLE 13. (Continued) Two-way synthesis table of parkland cover data made with 66/10 threshold values

Site	1	1	2	2	2	3	3	3	4	4	5	5	5	6	6	6	7	7	7	8	8	8	1	1	2	2	2	3	3	3	4	4	4	4	5	5	5	6	6	6	6	7	7	7	8	8	8
	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	R	P	P	P	P	P	P	P	P	P	P	R	P	P	P	P	P	P	P	P	P	P	P	P	P	P
Relevé	4	5	4	5	6	4	5	6	4	5	4	5	6	4	5	6	4	5	6	4	5	6	1	2	1	2	3	1	2	3	1	2	3	6	1	2	3	1	2	3	6	1	2	3	1	2	3
Species																																															
Styphelia tameiameiae			1		3	6	6	4		6			3						2			3			1	1	3		6	3			4	3	1		4	1		3	3			4		2	3
Rumex acetosella	6		6	1	6	6	6		6	6			6		6			6						6	6	6		6	1		6	6							6							
Paspalum dilatatum	6				6		6						6				1	1	6			1	2	2	2	1	6	1	3	2		6								6						
Carex wahuensis																									1	1	6	1			1	6	6		6	2	6	6	6	6		1	6	6	6	2	
Panicum tenuifolium																									6	1		1			1	1				1	1	6	6				1	6	2	6
Carex macloviana																							6						6			6			1			6	6								
Lotus angustissimus	6									6							6	6			1																			6							
Vaccinium reticulatum																			3		6	2																								1	2
Plantago lanceolata						6																							6	6	6															
Dodonaea sandwicensis																									6		3			1															6		
Dead wood											6	6																							2								1			
Andropogon virginicus								7																				7								7										
Cirsium vulgare																	7														7							7							
Cynodon dactylon									6		6						6																														

TABLE 13. (Continued) Two-way synthesis table of parkland cover data made with 66/10 threshold values

Site	1R	1R	2R	2R	2R	3R	3R	3R	4R	4R	5R	5R	5R	6R	6R	7R	7R	7R	8R	8R	8R	1P	1P	2P	2P	2P	3P	3P	3P	4P	4P	4P	4R	5P	5P	5P	6P	6P	6P	6R	7P	7P	7P	8P	8P	8P
Relevé	4	5	4	5	6	4	5	6	4	5	4	5	6	4	5	4	5	6	4	5	6	1	2	1	2	3	1	2	3	1	2	3	6	1	2	3	1	2	3	6	1	2	3	1	2	3
Species																																														
Coprosma ernodeoides																		6			6					2																					
Acacia koa																										7																7				
Medicago sp.																			6	6																											
Veronica plebeia											6	6																																			
Epilobium cinereum																											1																			
Centaurium umbellatum							6																																							
Tree root																																			7											
Rhacomitrium sp.																																								6					
Usnea sp.																																								7					
Goat droppings																																													6
Bromus rigidus																						7																							
Juncus tenuis																				7																									
Fragaria vesca																					6																									

TABLE 14. Two-way synthesis table of parkland cover data made with 66/20 threshold values

Site	2P	2P	3P	4P	4P	5P	5P	6P	6P	7P	8P	8P	1R	1R	2R	2R	2R	3R	3R	3R	4R	4R	5R	5R	5R	6R	6R	7R	7R	7R	8R	8R	8R	1P	1P	2P	3P	3P	4P	4R	5P	6P	6R	7P	7P	8P
Relevé	1	2	1	1	2	2	3	1	2	3	1	2	4	5	4	5	6	4	5	6	4	5	4	5	6	4	5	4	5	6	4	5	6	1	2	3	2	3	3	6	1	3	6	1	2	3
Species	*	*	*	*	*	*	*	*	*	*	*	*																																			
Carex wahuensis	1	1	1	1	6	2	6	6	6	6	6	2																								6			6		6	6		1	6	
Panicum tenuifolium	6	1	1	1	1	1	1	6	6	1	6	2																																			6
	*	*	*	*	*	*	*	*	*	*	*	*																																		
													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*													
Sporobolus africanus	6	6											2	2	3	3	2	2	3	2	3	3	3	2	2	2	2	3	3	2	2	1	1						2							
Cattle feces													6	1	1	1	6	6	1	6	1	2	1	1	1	6	6	1	1	6	1	1	6						6			6				
Axonopus affinis													6	1	2	1	2	2	2	1	2	2	6	2	1	1	1	2	2	6	2	6	6						2							
Eragrostis brownei											6				6		6	6	6	6				1	6	2	2	6	6	2	1	2	2												
Pennisetum clandestinum													3	3	6	1		1	1		2	2	3	2	1			2	2	6	6	3													
													*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*													
Litter	2	2	2	3	3	3	2	2	3	2	2	2	3	3	3	3	2	3	3	2	3	3	3	3	2	3	3	2	2	2	3	3	2	2	3	2	3	2	2	2	3	2	2	2	3	2
Hypochoeris radicata	1	1	1	1	1	6	6	1	6	1	1	2	1	6	1	1	1	1	1	1	1			6	1	6	1	6	6	2	6	1	1	6	6	6	6	6	1	6	1	1	6	1	1	1
Anthoxanthum odoratum	2	2	2	1	2	2	2	2	1	6		6	2	2	2	2	2	2	2	1	2	1	2	2	1	2	2	2	2	1	2	2	2	6	1	6	1	6	6	1	2	6	2			
Bare soil	2	2	2	2	1	2	1	2	2	1	2	2			1	1	2	2	2	1		1		1	1	2	2	1	6	1	1	6	2		6	1		1	1	2	1	1	2	1	1	2
Exposed rock	6	1	1	1	6	1	1	1	2	1	2	1			6	1	2	1	2	1	6	1		1	1	1	1		1	1	6	6	2			6		6	6	1	1	1	1	6	6	2
Pteridium aquilinum	2	2	2	2	1	6	6	1				6	6	6	2	1	1	1	6	1	2	2	6	1	1	6	1							2	2	1	1	1	1	1	1	1	6			6

TABLE 14. (Continued) Two-way synthesis table of parkland cover data made with 66/20 threshold values

Site	2P	2P	3P	4P	4P	5P	5P	6P	6P	7P	8P	8P	1R	1R	2R	2R	2R	3R	3R	3R	4R	4R	5R	5R	5R	6R	6R	7R	7R	7R	8R	8R	1P	1P	2P	3P	3P	4P	4R	5P	6P	6R	7P	7P	8P
Relevé	1	2	1	1	2	2	3	1	2	3	1	2	4	5	4	5	6	4	5	6	4	5	4	5	6	4	5	4	5	6	4	5	6	1	2	3	2	3	3	3	6	1	3	6	1	2	3
Species																																														
Deschampsia australis	2	2	2	3	3	3	2	3	2	2	3	3					1			2					1	2	2							2	1	1	2	2	1	3	2	2	4	4	2
Holcus lanatus	2	2	2	2	2	1	2	2	3	2	2	2	6		6														6				2	3	1	3	2	1		1	1		1	6	1
Styphelia tameiameiae	1	1					4	1		4		2			1		3	6	6	4		6			3				2			3			3	6	3	4	3	1	3	3			3
Rumex acetosella	5	6	6	6	6				6				6		6	1	6	6	6		6	6			6		6		6					6		1									
Paspalum dilatatum	2	1	1		6								6				6		6						6			1	1	6			1	2	2	6	3	2			6			
Carex macloviana					6			6	6																								6			6				1				
Lotus angustissimus													6									6						6	6		1										6			
Vaccinium reticulatum												1																		3		6	2											2
Plantago lanceolata				6														6																		6	6							
Dodonaea sandwicensis	6											6																							3		1							
Dead wood											1												6	6																2				
Andropogon virginicus			7			7														7																								
Cirsium vulgare					7				7																			7															
Cynodon dactylon																						6		6				6															
Coprosma ernodeoides																														6		6						2					

TABLE 14. (Continued) Two-way synthesis table of parkland cover data made with 66/20 threshold values

Site	2 P	2 P	3 P	4 P	4 P	5 P	5 P	6 P	6 P	7 P	8 P	8 P	1 R	1 R	2 R	2 R	2 R	3 R	3 R	3 R	4 R	4 R	5 R	5 R	5 R	6 R	6 R	7 R	7 R	7 R	8 R	8 R	8 R	1 P	1 P	2 P	3 P	3 P	4 P	4 R	5 P	6 P	6 R	7 P	7 P	8 P
Relevé	1	2	1	1	2	2	3	1	2	3	1	2	4	5	4	5	6	4	5	6	4	5	4	5	6	4	5	4	5	6	4	5	6	1	2	3	2	3	3	6	1	3	6	1	2	3
Species																																														
Acacia koa																																				7								7		
Medicago sp.																															6	6														
Veronica plebeia																							6	6																						
Epilobium cinereum			1																																											
Centaurium umbellatum																			6																												
Tree root							7																																							
Rhacomitrium sp.																																												6		
Usnea sp.																																												7		
Goat droppings																																														6
Bromus rigidus																																		7												
Juncus tenuis																															7														
Fragaria vesca																																6													

TABLE 15. Data from park soil pits

Site	Elevation	Depth of Soil Pit (cm)	Horizon	Thickness of Horizon (cm)	Color of Air Dried Soil	Munsell Color Notation
1	4600'	77	A	17	V. dk. gr. brown	10YR 3/2
			B	60	Dark brown	10YR 3/3
2	4800'	56	A	31	V. dk. gr. brown	10YR 3/2
			B	25	Dark brown	10YR 3/3
3	500'	54	A	21	V. dk. gr. brown	10YR 3/2
			B	33	V. dark brown	10YR 2/2
4	5200'	29	A	11	Dark brown	7.5YR 3/2
			B	18	Brown/dk. brown	7.5YR 4/4
5	5400'	15	A	10	Dark brown	7.5YR 3/2
			B	5	Brown/dk. brown	7.5YR 4/4
6	5600'	28	A	15	V. dk. gr. brown	10YR 3/2
			B	13	Dark brown	10YR 3/3
7	5800'	39	A	18	Dk. red. brown	5YR 3/2
			B	21	Dk. red. brown	5YR 3/4
8	6000'	31	A	15	V. dk. gr. brown	10YR 3/2
			B	16	V. dark brown	10YR 2/2

TABLE 16. Data from ranch soil pits

Site	Elevation	Depth of Soil Pit (cm)	Horizon	Thickness of Horizon (cm)	Color of Air Dried Soil	Munsell Color Notation
1	4600'	31	A	31	Dk. red. brown	5YR 2.5/2
2	4800'	17	A	17	Dark brown	7.5YR 3/2
3	5000'	36	A	36	Dark brown	7.5YR 3/2
4	5200'	43	A	14	V. dk. gr. brown	10YR 3/2
			B	29	Dark brown	10YR 3/3
5	5400'	29	A	10	V. dk. gr. brown	10YR 3/2
			B	19	Dk. yel. brown	10YR 3/4
6	5600'	12	A	5	Dk. red. brown	5YR 3/2
			B	7	Dk. red. brown	5YR 3/4
7	5800'	24	A	9	Dk. red. brown	5YR 2.5/2
			B	15	Dk. red. brown	5YR 3/2
8	6000'	6	A	6	Dark brown	7.5YR 3/2

TABLE 17. Soil depths (cm) in park and ranch relevés

Site	Elevation	Park		Ranch	
		Mean	Standard Deviation	Mean	Standard Deviation
1	4600'	62.16	23.63	51.60	32.17
2	4800'	54.85	28.32	17.84	11.31
3	5000'	42.72	16.48	20.76	15.66
4	5200'	26.28	14.18	37.16	23.24
5	5400'	15.76	7.91	27.52	16.94
6	5600'	26.82	17.41	11.70	6.76
7	5800'	38.44	21.17	10.72	6.87
8	6000'	29.44	19.72	8.68	5.00

TABLE 18. Percentage moisture of park and ranch soils at field capacity (0.3 bar) and permanent wilting percentage (15 bar)

Site	Elevation	Horizon	Park		Ranch	
			% at FC	% at PWP	% at FC	% at PWP
1	4600'	A	46.0	26.4	50.2	35.0
1	4600'	B	56.5	38.0	--	--
2	4800'	A	35.5	25.0	45.3	26.5
2	4800'	B	49.2	40.0	--	--
3	5000'	A	50.6	34.4	41.5	26.5
3	5000'	B	43.8	49.2	--	--
4	5200'	A	46.6	28.4	60.9	40.9
4	5200'	B	19.3	17.4	54.4	37.4
5	5400'	A	39.1	21.2	42.8	35.2
5	5400'	B	25.5	22.9	55.8	54.7
6	5600'	A	48.9	35.3	51.0	33.5
6	5600'	B	19.1	18.0	40.3	27.5
7	5800'	A	51.4	34.7	83.9	68.0
7	5800'	B	55.0	39.6	31.9	24.6
8	6000'	A	47.1	25.5	63.5	45.2
8	6000'	B	32.9	24.5	--	--

TABLE 19. Bulk density (g/cm^3), pH, and percentage organic carbon of soils in relevés

Site	Elevation	Horizon	Park			Ranch		
			BD	pH	% OC	BD	pH	% OC
1	4600'	A	0.68	6.2	1.94	0.68	5.8	6.37
1	4600'	B	--	6.3	1.90	--	--	--
2	4800'	A	1.00	6.5	0.71	0.81	6.0	3.32
2	4800'	B	--	6.6	2.19	--	--	--
3	5000'	A	0.77	5.9	7.36	0.58	6.0	6.28
3	5000'	B	--	6.0	5.57	--	--	--
4	5200'	A	0.87	6.2	1.40	0.66	5.7	9.88
4	5200'	B	--	6.3	2.69	--	6.1	5.48
5	5400'	A	0.74	5.7	1.78	0.70	5.6	8.30
5	5400'	B	--	6.0	3.87	--	5.9	9.32
6	5600'	A	0.61	5.9	8.65	0.66	5.6	9.44
6	5600'	B	--	6.5	3.42	--	6.0	1.70
7	5800'	A	0.74	5.6	3.84	0.48	5.6	16.83
7	5800'	B	--	6.0	2.95	--	5.5	10.70
8	6000'	A	0.78	6.1	0.75	0.53	5.7	9.75
8	6000'	B	--	6.2	5.09	--	--	--

TABLE 20. Fertility of soils in park and ranch relevés[a]

Site	Elevation	Relevé Location	Horizon	P lb/Acre	K lb/Acre	Ca lb/Acre	Mg lb/Acre
1	4600'	Ranch	A	<25	240	4000	250
1	4600'	Park	A	<25	240	4000	250
1	4600'	Park	B	Trace	320	4000	250
2	4800'	Ranch	A	<25	160	4000	250
2	4800'	Park	A	<25	320	4000	250
2	4800'	Park	B	Trace	320	5000	250
3	5000'	Ranch	A	Trace	320	4000	250
3	5000'	Park	A	Trace	240	3000	250
3	5000'	Park	B	Trace	160	3000	250
4	5200'	Ranch	A	25	320	4000	250
4	5200'	Ranch	B	<25	120	2000	250
4	5200'	Park	A	<25	160	4000	250
4	5200	Park	B	<25	80	2000	250
5	5400'	Ranch	A	Trace	80	2000	250
5	5400'	Ranch	B	Trace	80	2000	250

TABLE 20. (Continued) Fertility of soils in park and ranch relevés

Site	Elevation	Relevé Location	Horizon	P lb/Acre	K lb/Acre	Ca lb/Acre	Mg lb/Acre
5	5400'	Park	A	<25	160	4000	250
5	5400'	Park	B	Trace	80	1000	250
6	5600'	Ranch	A	25	320	4000	250
6	5600'	Ranch	B	Trace	80	500	<250
6	5600'	Park	A	<25	240	4000	250
6	5600'	Park	B	<25	240	4000	250
7	5800'	Ranch	A	Trace	160	4000	250
7	5800'	Ranch	B	Trace	80	2000	250
7	5800'	Park	A	<25	120	4000	250
7	5800'	Park	B	Trace	80	500	<250
8	6000'	Ranch	A	Trace	160	4000	250
8	6000'	Park	A	<25	160	4000	250
8	6000'	Park	B	Trace	40	5000	<250

[a]Determined by the Soil Testing Service of the University of Hawaii - U.S.D.A. Cooperative Extension Service using a rapid turbidometric or colorimetric method.

FIG. 1. A map of Hawaii Volcanoes National Park (delimiting the study area) and (showing the location of 13 of the study sites).

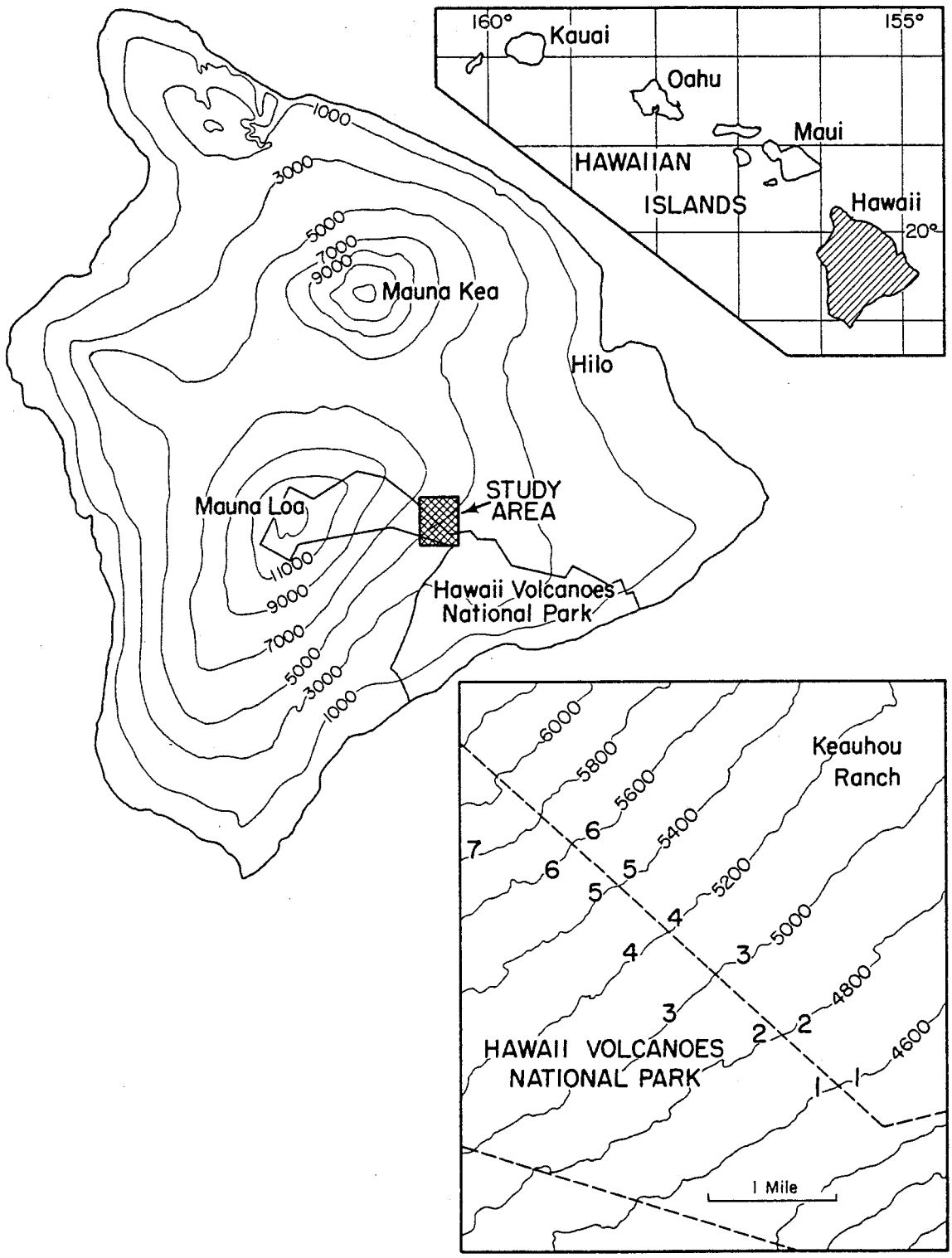

160°
155°
Kauai
Oahu
Maui
HAWAIIAN
ISLANDS
Hawaii
20°
1000
3000
5000
7000
9000
Mauna Kea
Hilo
Mauna Loa
STUDY
AREA
11000
9000
7000
5000
3000
1000
Hawaii Volcanoes
National Park
6000
5800
5600
5400
5200
5000
4800
4600
Keauhou
Ranch
HAWAII VOLCANOES
NATIONAL PARK
1 Mile

FIG. 2. Percentage cover of major plant species in grassland relevēs of park and ranch.

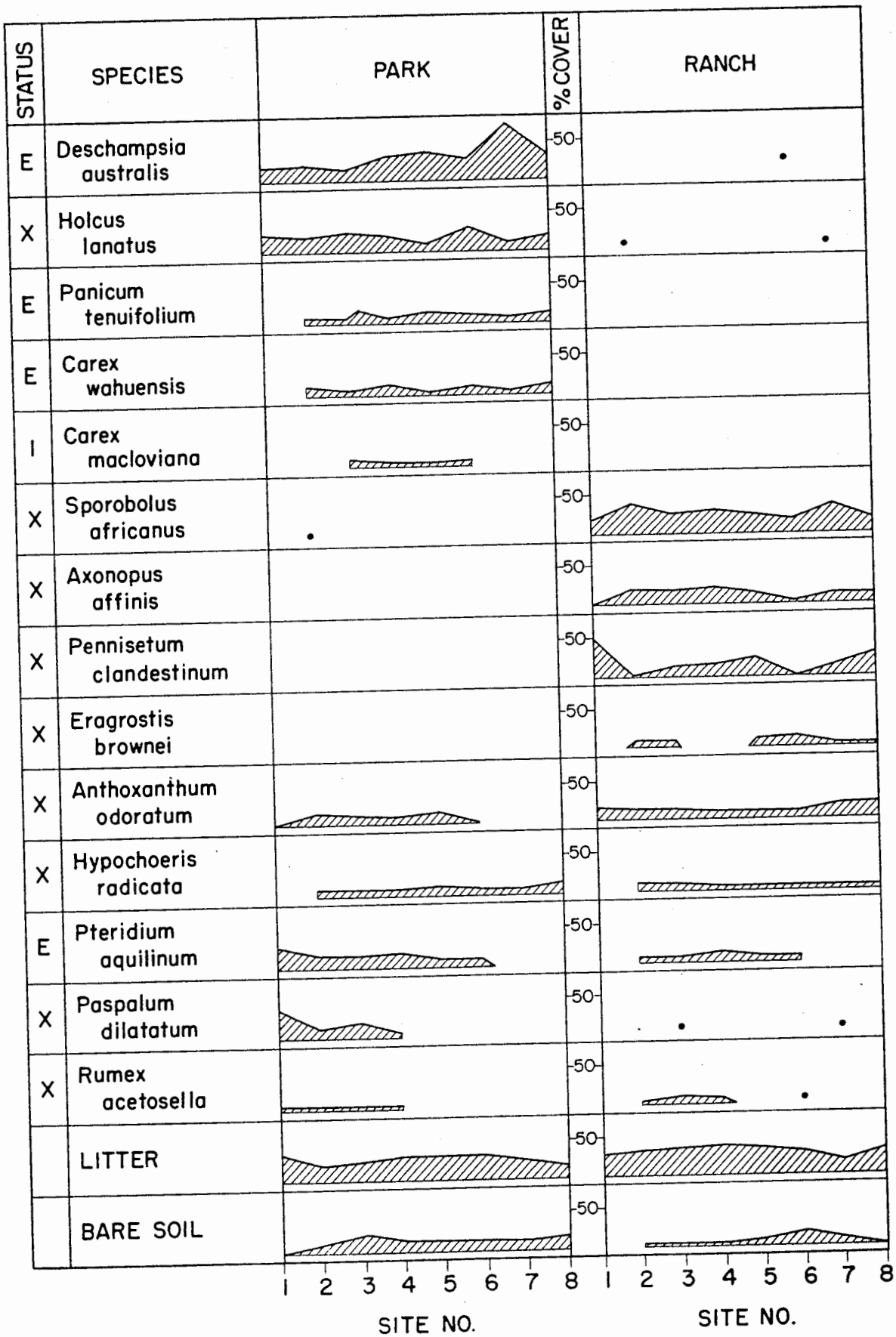

STATUS
SPECIES
PARK
% COVER
RANCH
E
Deschampsia australis
X
Holcus lanatus
E
Panicum tenuifolium
E
Carex wahuensis
I
Carex macloviana
X
Sporobolus africanus
X
Axonopus affinis
X
Pennisetum clandestinum
X
Eragrostis brownei
X
Anthoxanthum odoratum
X
Hypochoeris radicata
E
Pteridium aquilinum
X
Paspalum dilatatum
X
Rumex acetosella
LITTER
BARE SOIL
50
1 2 3 4 5 6 7 8
SITE NO.
1 2 3 4 5 6 7 8
SITE NO.

FIG. 3. Percentage cover of major plant species in shrub relevēs of park and ranch.

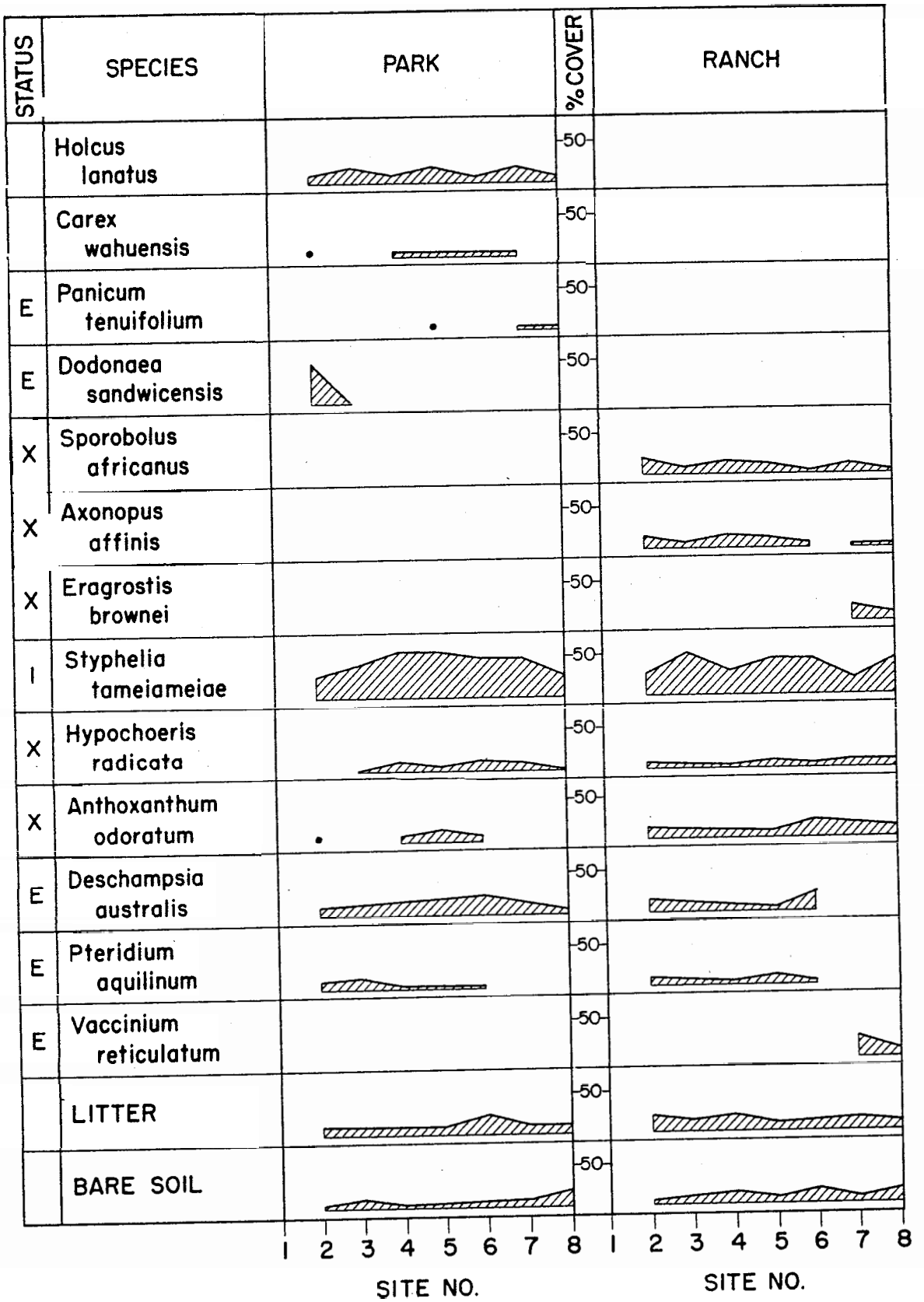

STATUS
SPECIES
PARK
% COVER
RANCH
Holcus lanatus
Carex wahuensis
Panicum tenuifolium
Dodonaea sandwicensis
Sporobolus africanus
Axonopus affinis
Eragrostis brownei
Styphelia tameiameiae
Hypochoeris radicata
Anthoxanthum odoratum
Deschampsia australis
Pteridium aquilinum
Vaccinium reticulatum
LITTER
BARE SOIL
E
X
I
50
1 2 3 4 5 6 7 8
SITE NO.
SITE NO.

FIG. 4. Dendrograph of parkland relevēs based on Jaccard's index of similarity.

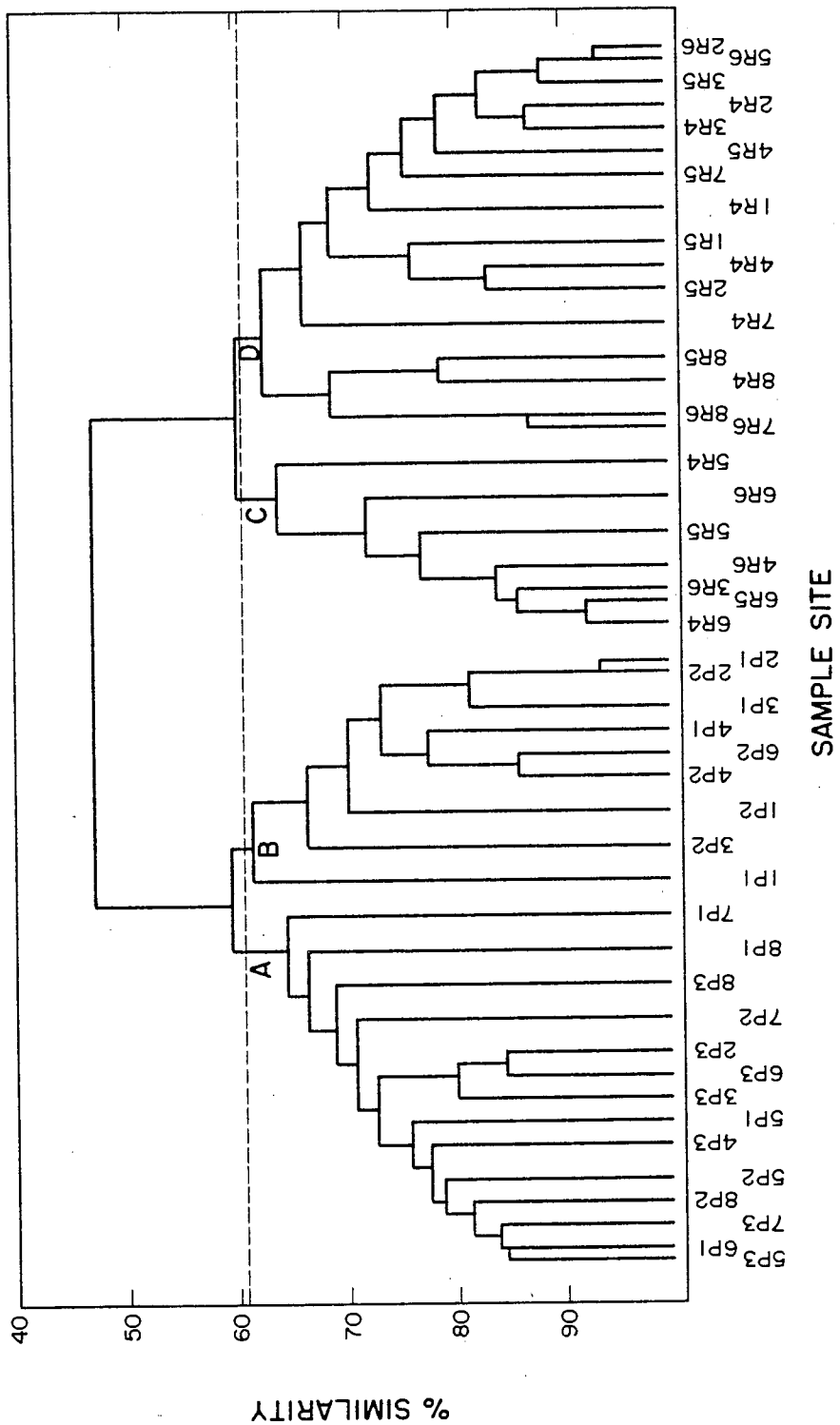
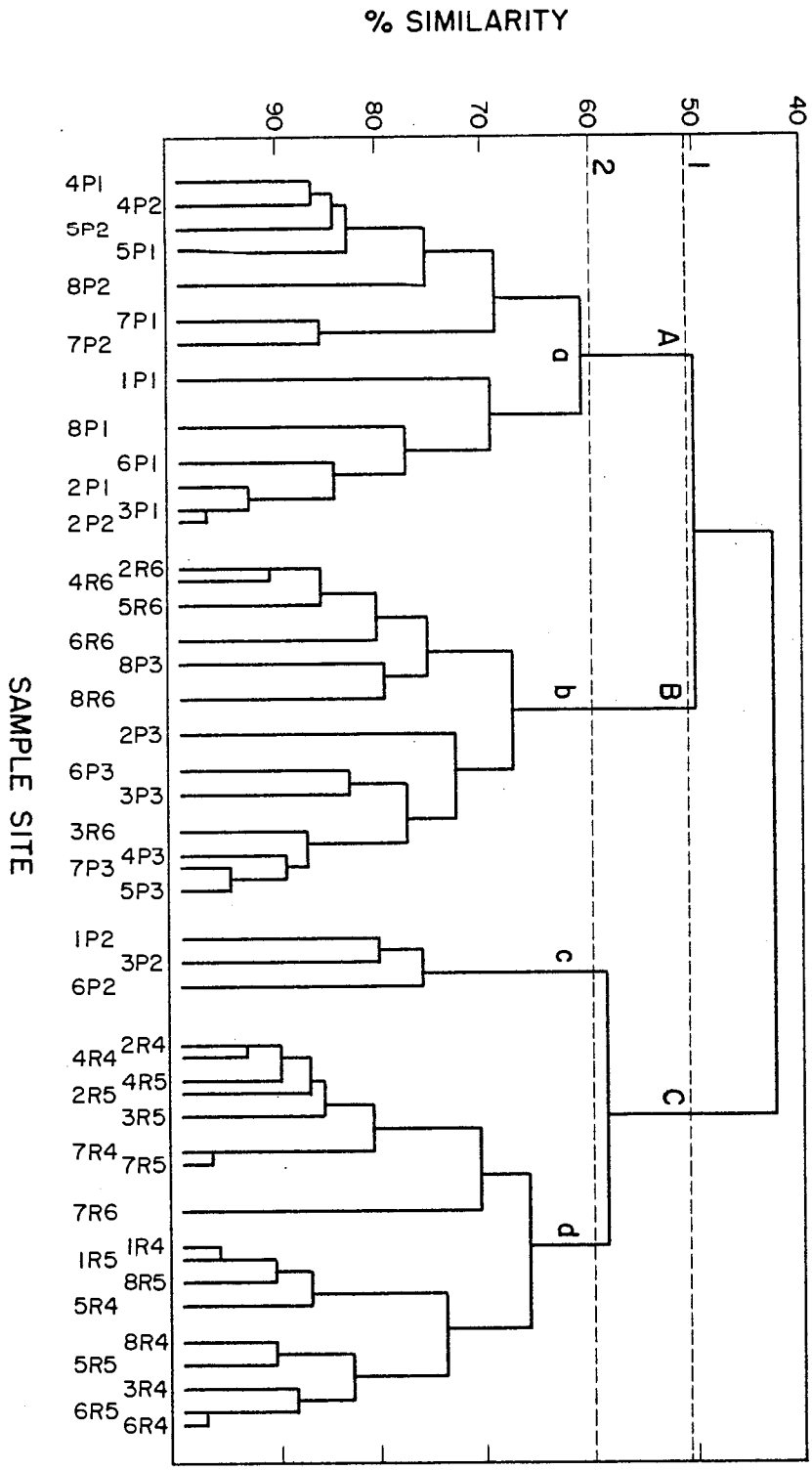

% SIMILARITY
40
50
60
70
80
90
A
B
C
D
SAMPLE SITE
5P3
6P1
7P3
8P2
5P2
4P3
5P1
3P3
6P3
2P3
7P2
8P3
8P1
7P1
1P1
3P2
1P2
4P2
6P2
4P1
3P1
2P2
2P1
6R4
6R5
3R6
4R6
5R5
6R6
5R4
7R6
8R6
8R4
8R5
7R4
2R5
4R4
1R5
1R4
7R5
4R5
3R4
2R4
3R5
5R6
2R6

FIG. 5. Dendrograph of parkland relevēs based on Sorensen's quantitative index of similarity.


% SIMILARITY
90
80
70
60
50
40
2
1
SAMPLE SITE
4P1
4P2
5P2
5P1
8P2
7P1
7P2
1P1
8P1
6P1
2P1
3P1
2P2
4R6
2R6
5R6
6R6
8P3
8R6
2P3
6P3
3P3
3R6
4P3
7P3
5P3
1P2
3P2
6P2
4R4
2R4
4R5
2R5
3R5
7R4
7R5
7R6
1R4
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b
c
d
A
B
C

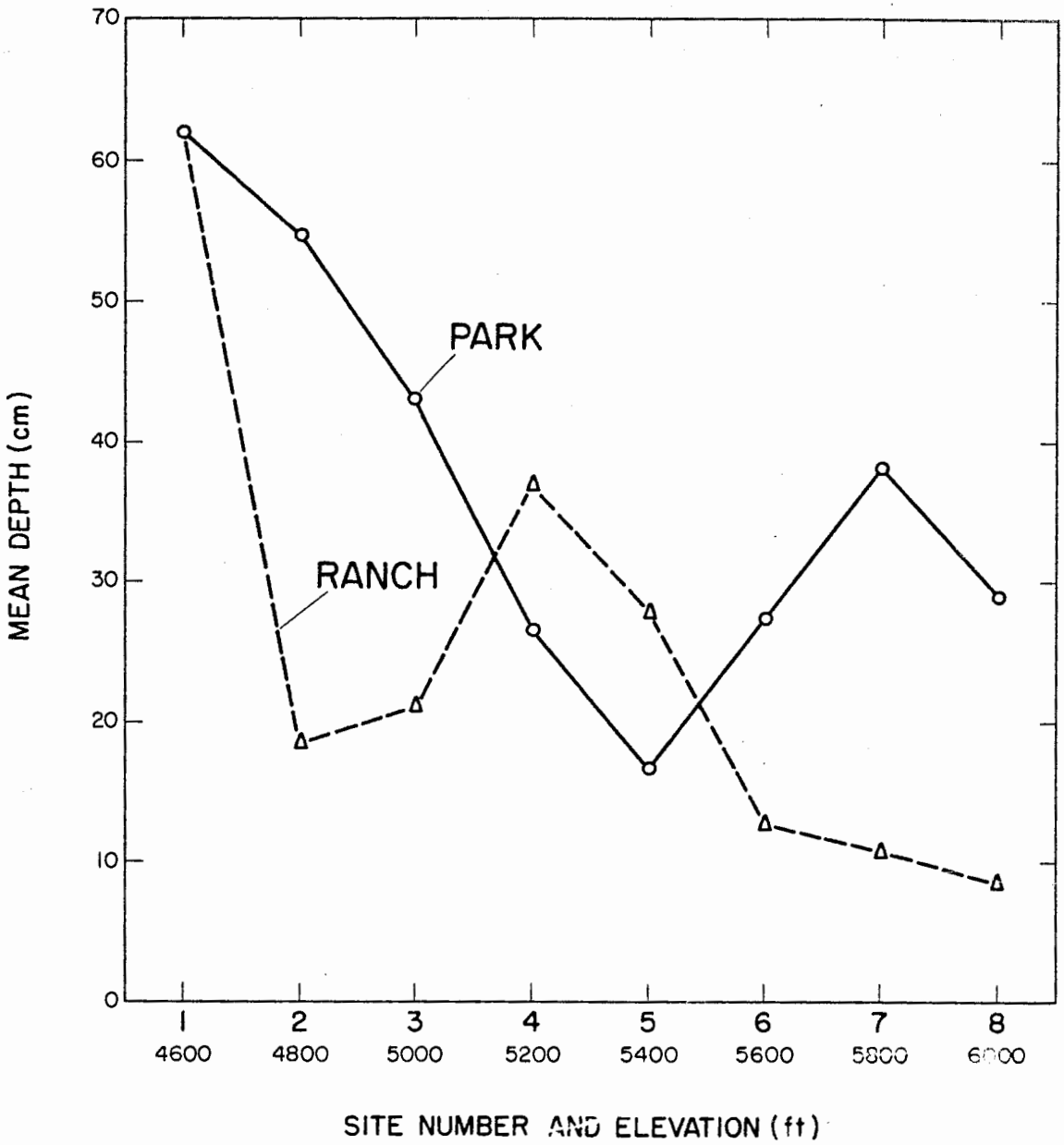


FIG. 6. Mean soil depth at park and ranch sites.

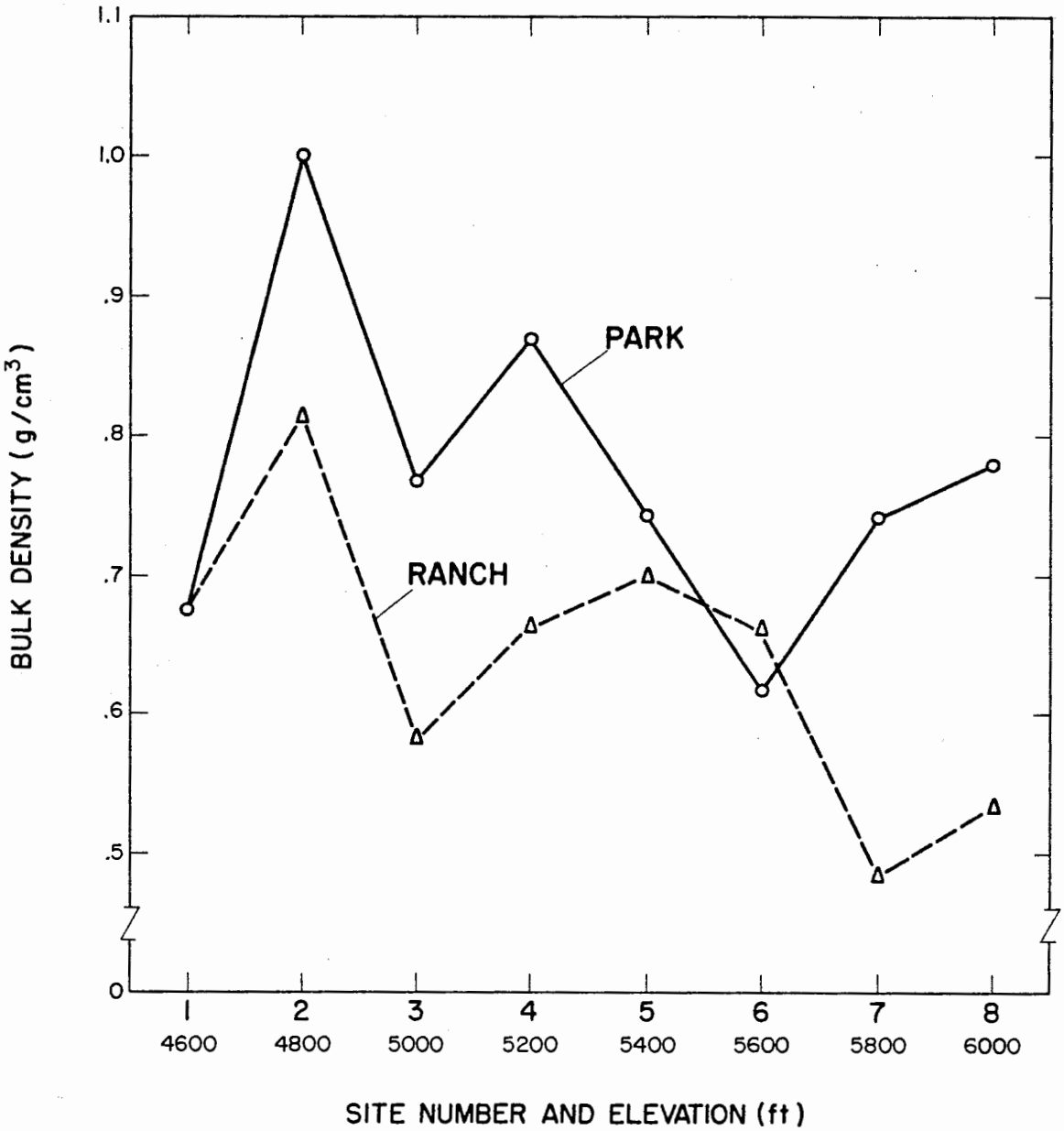


FIG. 7. Bulk density of soil at park and ranch sites (A horizon).

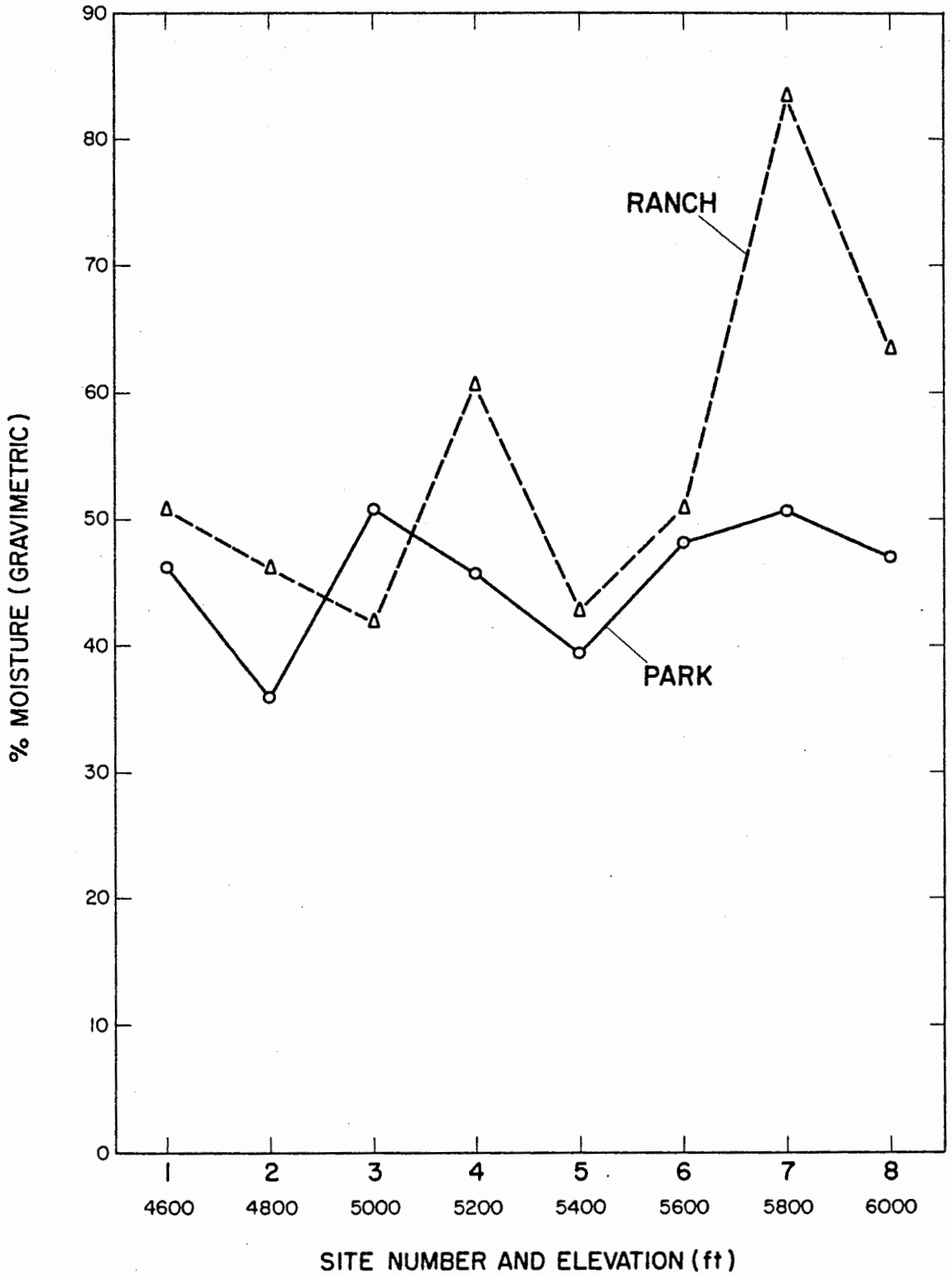


FIG. 8. Water content at field capacity (0.3 bar) of A horizon soils from park and ranch sites.

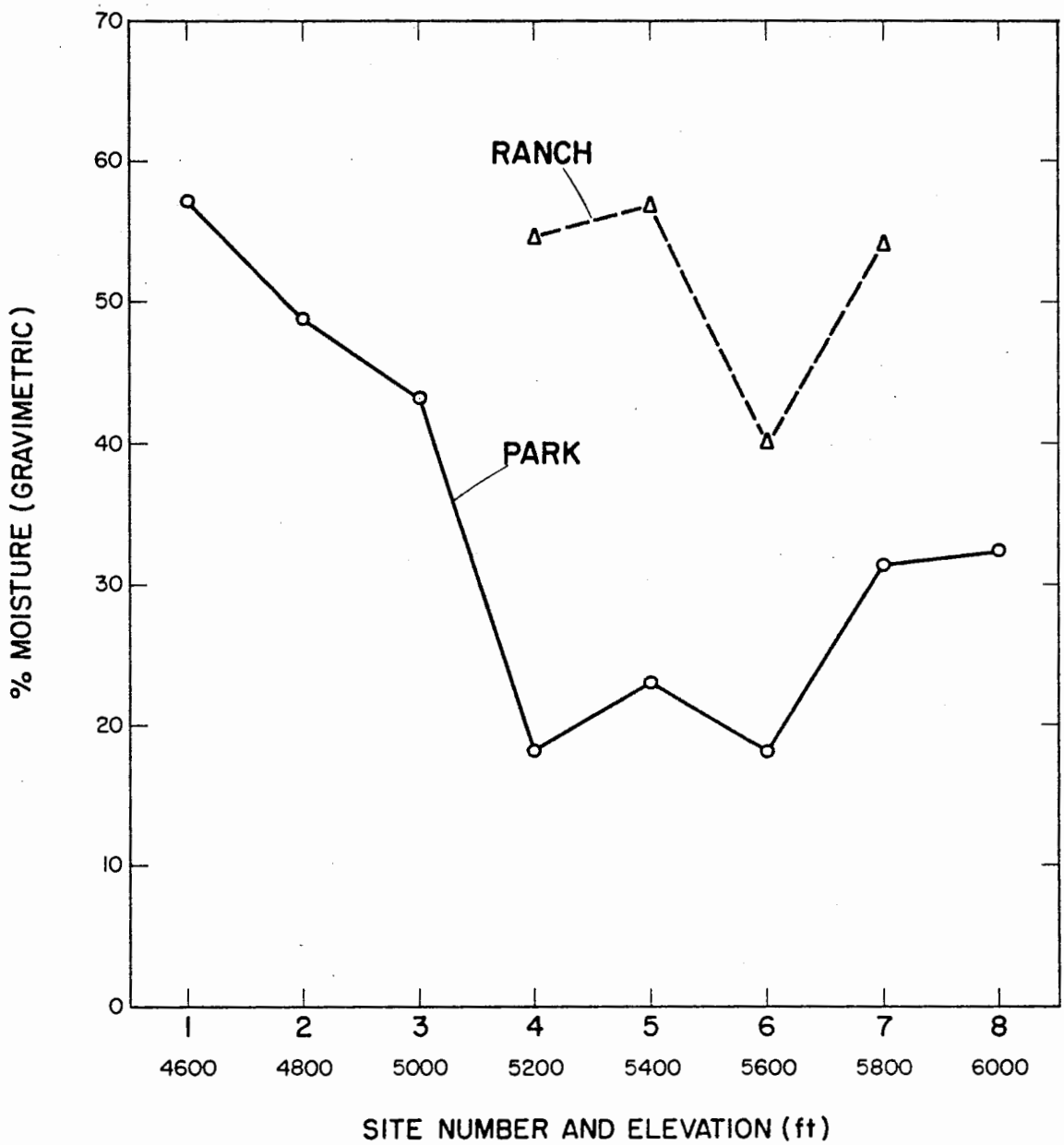


FIG. 9. Water content at field capacity (0.3 bar) of B horizon soils from park and ranch sites.

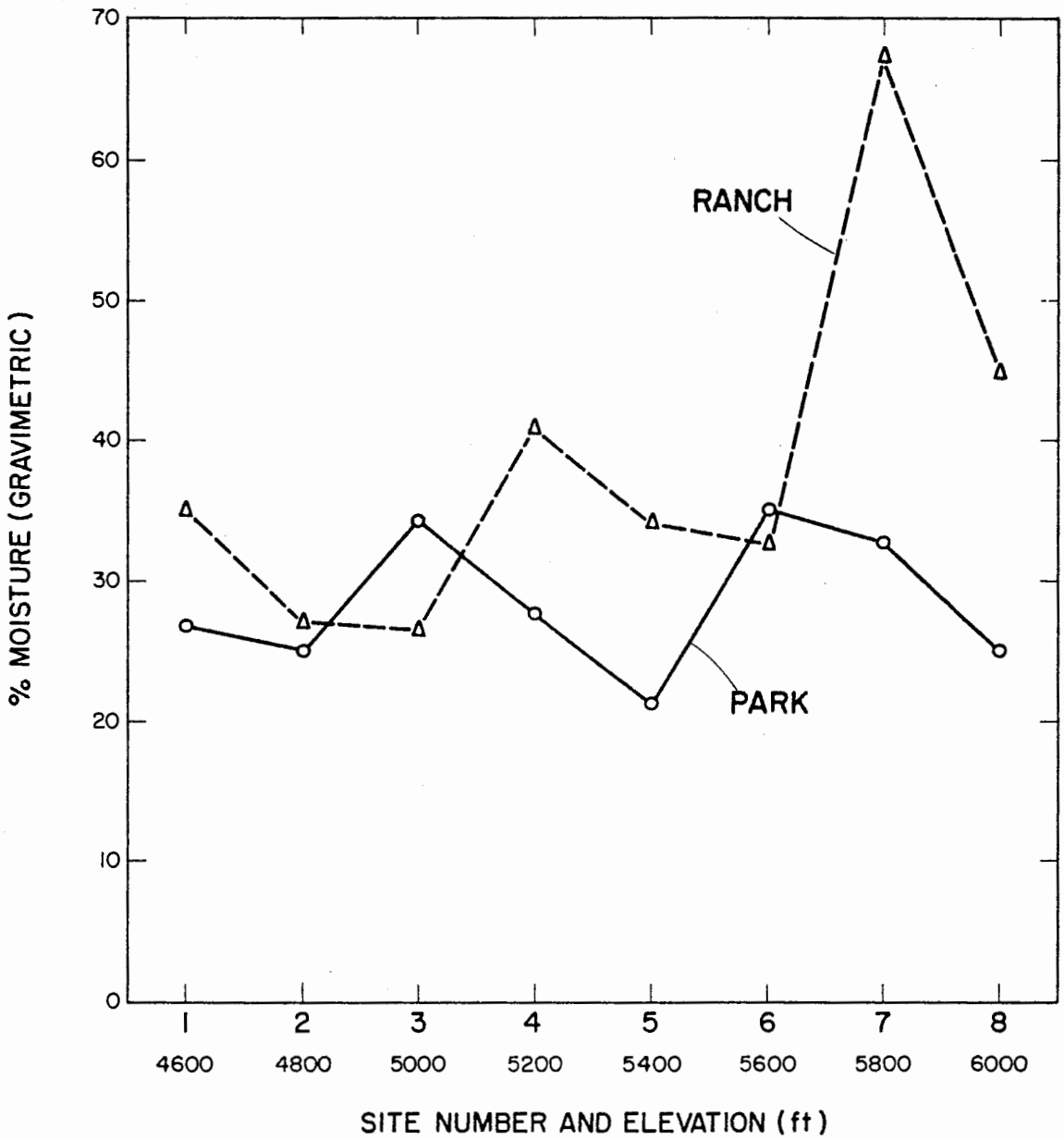


FIG. 10. Water content at permanent wilting percentage (15 bar) of A horizon soils from park and ranch sites.

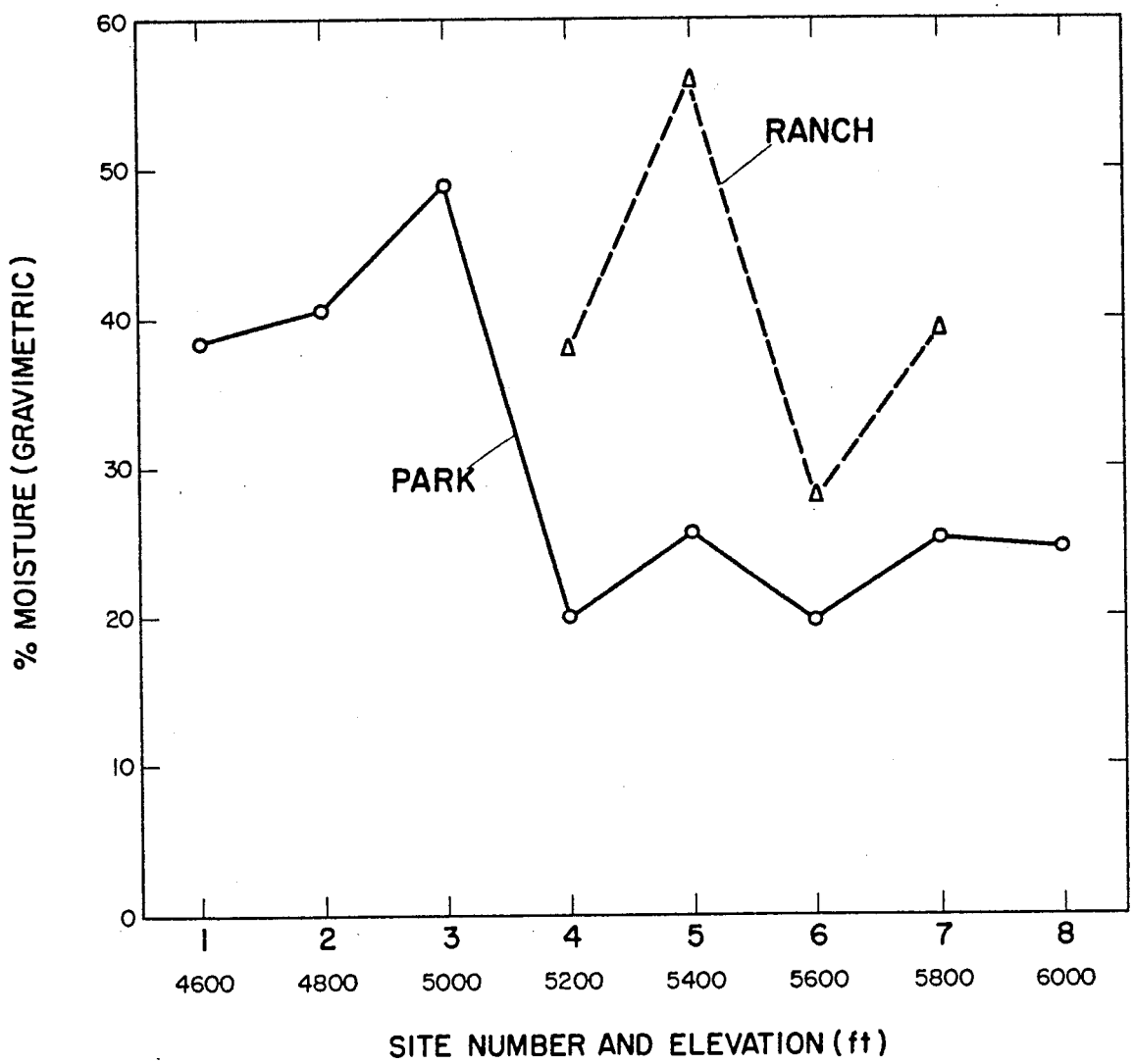


FIG. 11. Water content at permanent wilting percentage (15 bar) of B horizon soils from park and ranch sites.

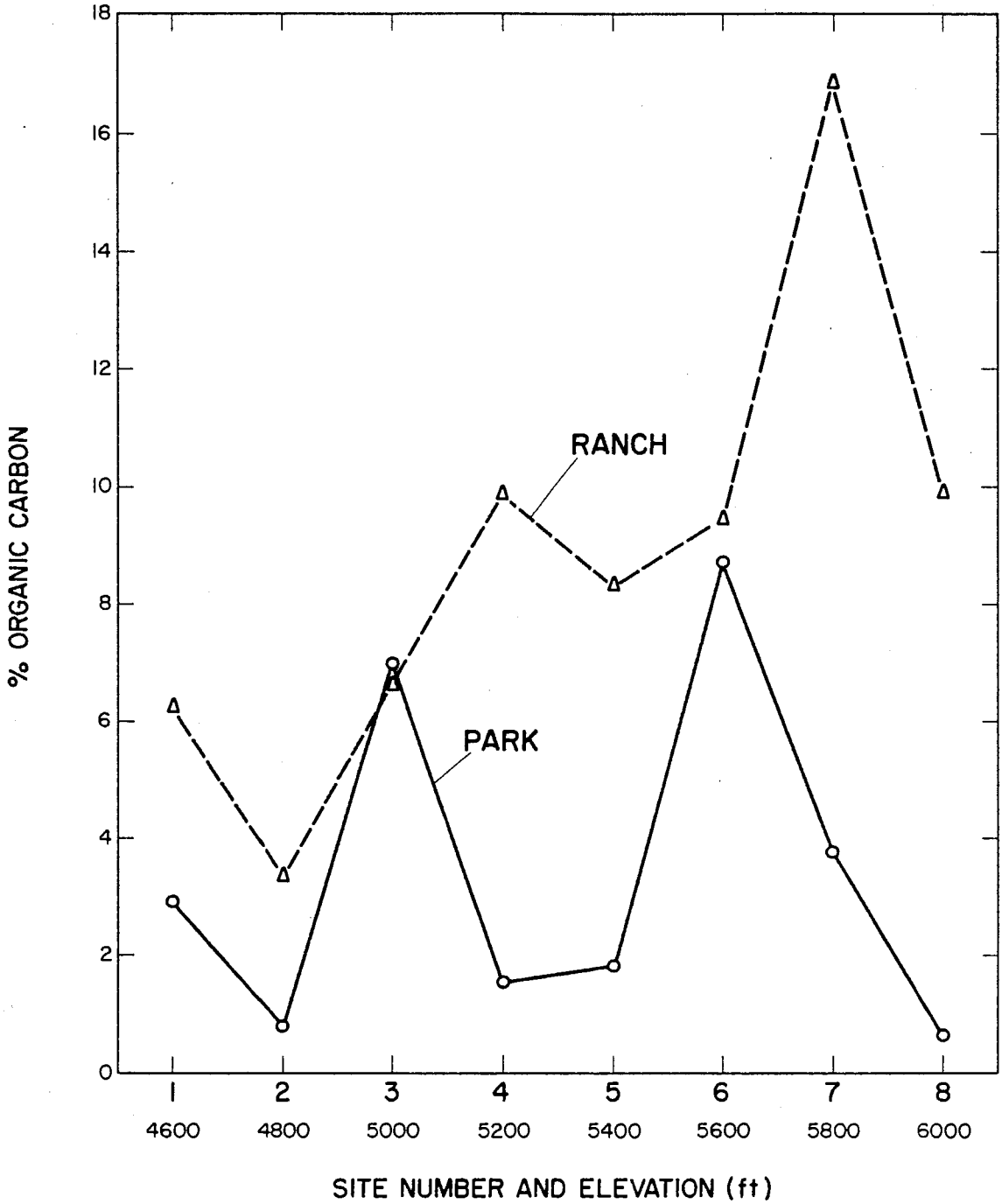


FIG. 12. Percentage organic carbon of A horizon soils from park and ranch relevēs.

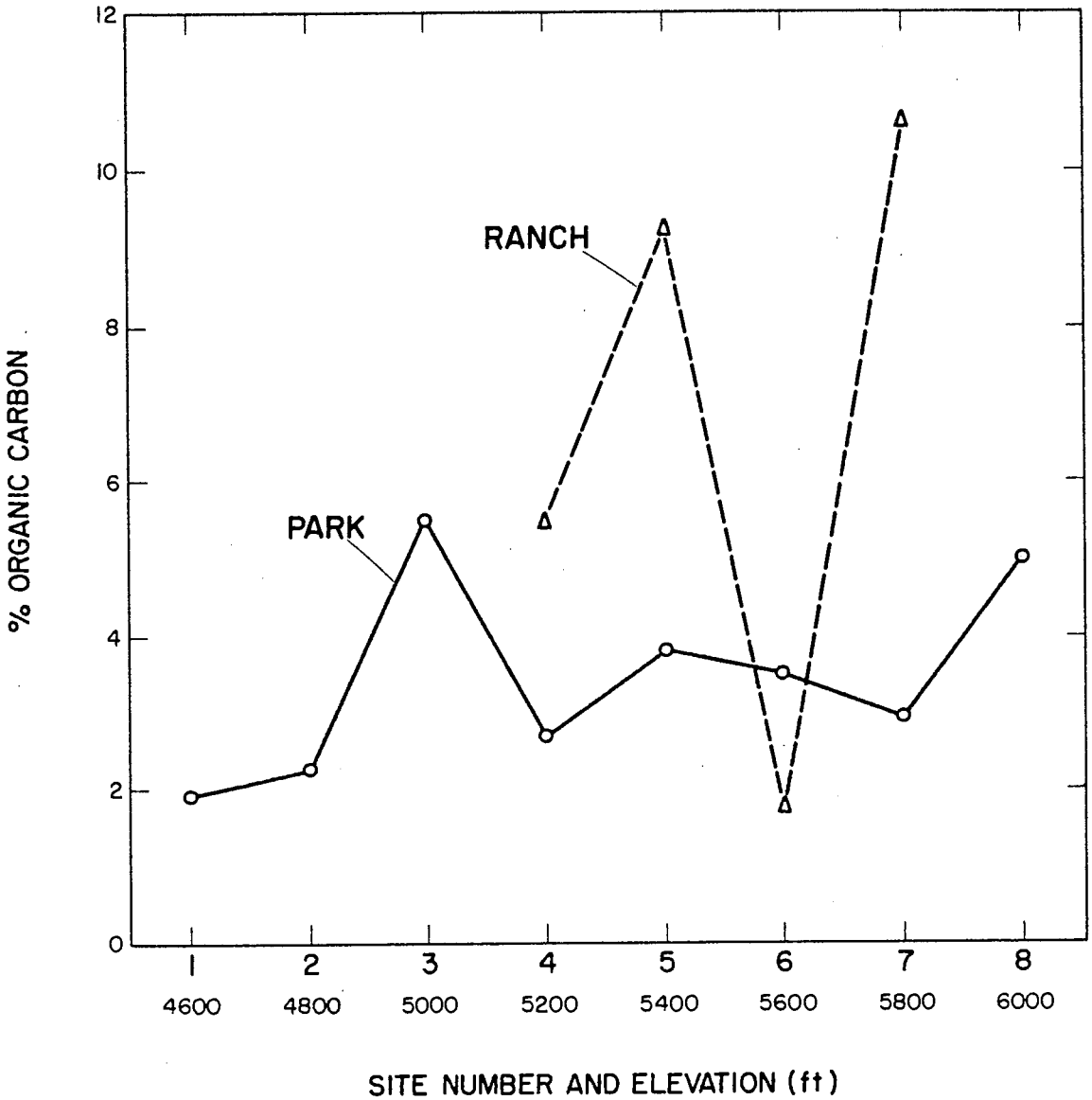


FIG. 13. Percentage organic carbon of B horizon soils from park and ranch relevēs.

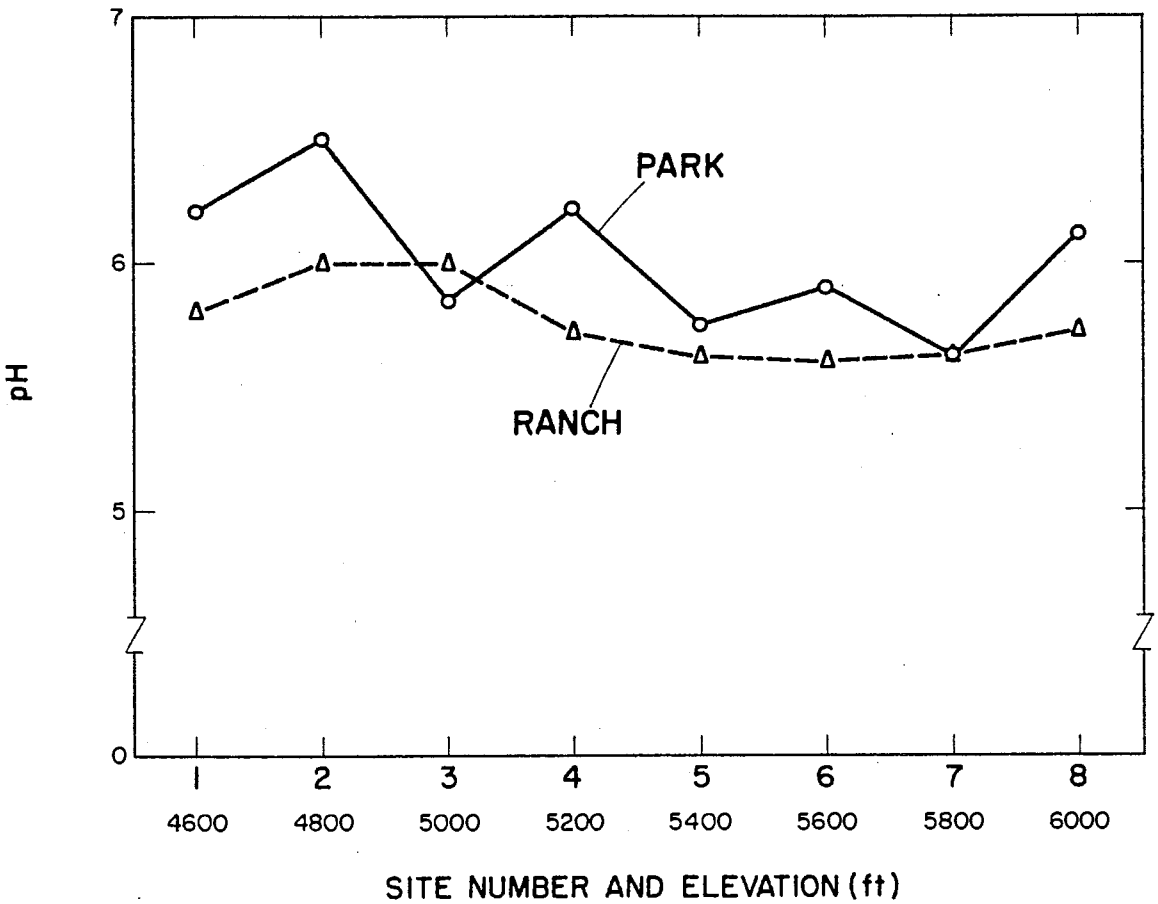


FIG. 14. pH values for A horizon soils of park and ranch relevēs.

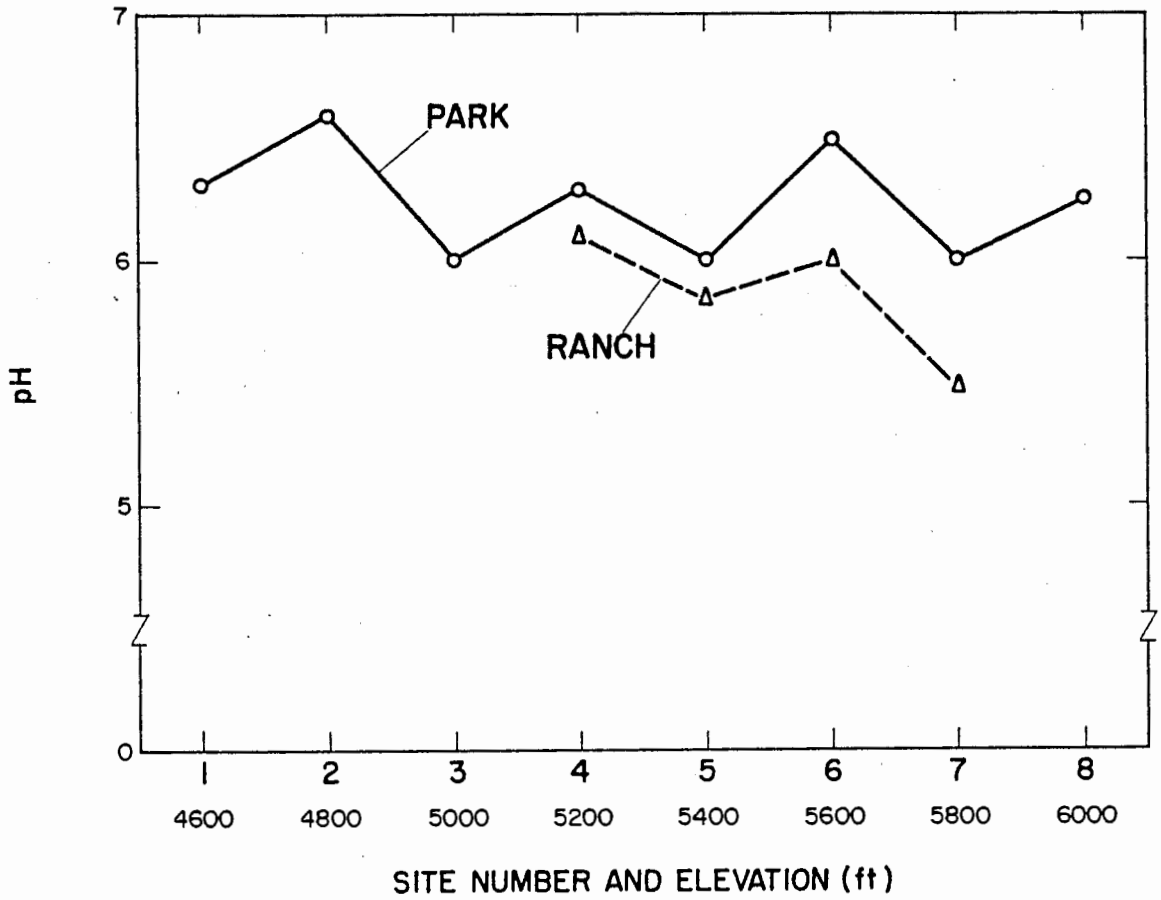


FIG. 15. pH values for B horizon soils of park and ranch relevēs.

FIG. 16. Fertility levels of four nutrients in A horizon soils of park and ranch relevēs.

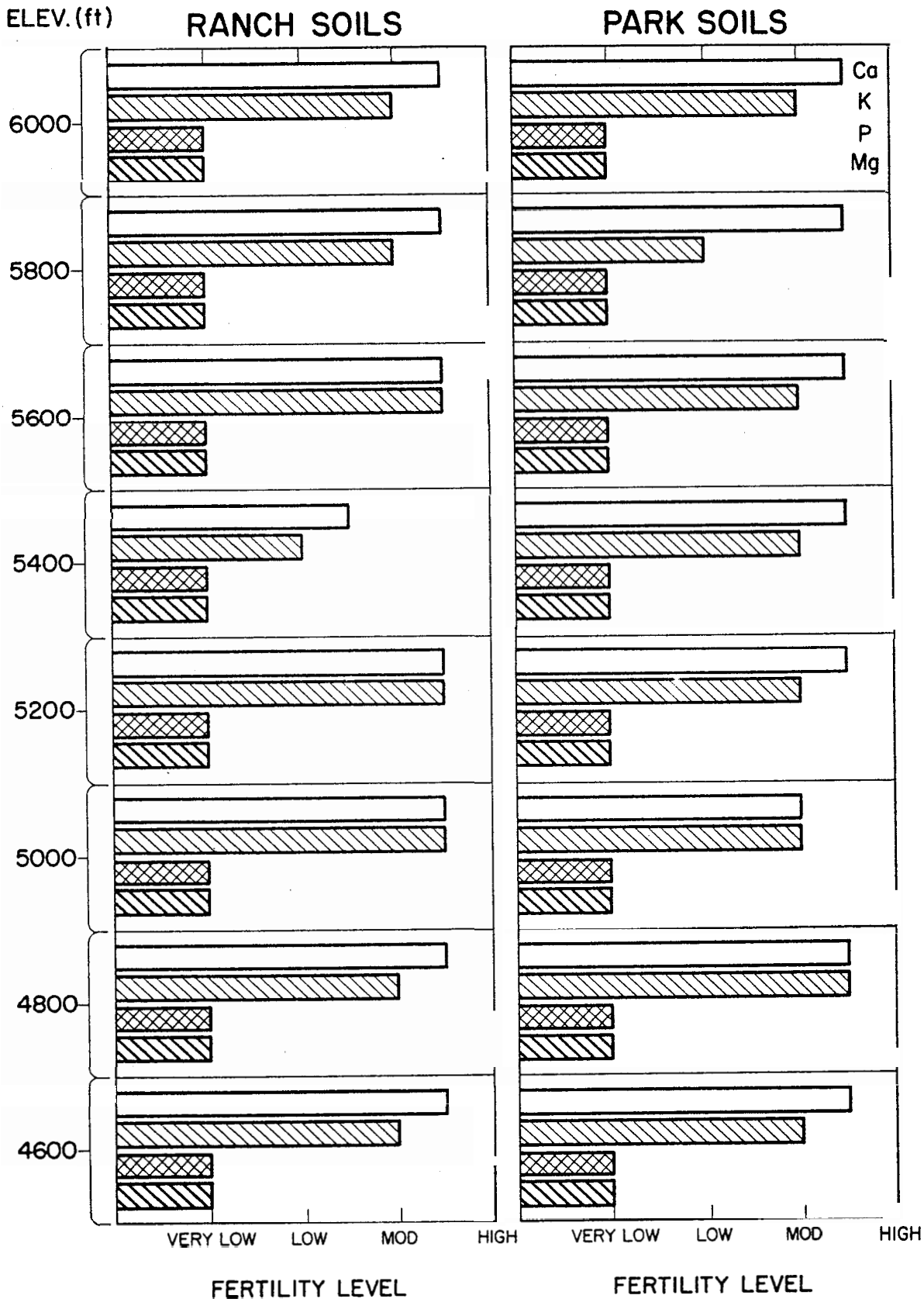

ELEV. (ft)
RANCH SOILS
PARK SOILS
Ca
K
P
Mg
6000
5800
5600
5400
5200
5000
4800
4600
VERY LOW
LOW
MOD
HIGH
VERY LOW
LOW
MOD
HIGH
FERTILITY LEVEL
FERTILITY LEVEL

FIG. 17. Fertility levels of four nutrients in B horizon soils of park and ranch relevēs.

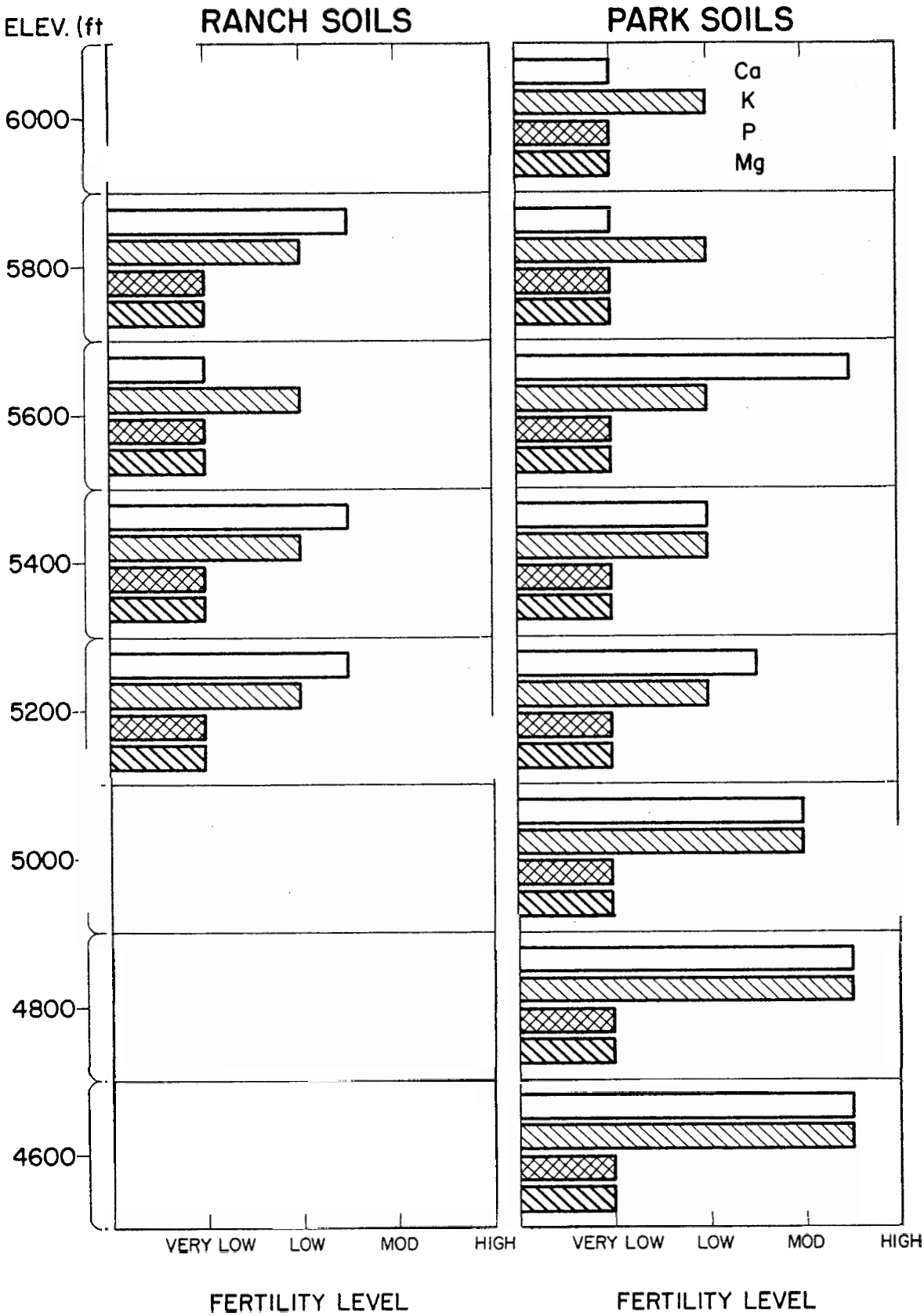

ELEV. (ft
RANCH SOILS
PARK SOILS
Ca
K
P
Mg
6000
5800
5600
5400
5200
5000
4800
4600
VERY LOW
LOW
MOD
HIGH
VERY LOW
LOW
MOD
HIGH
FERTILITY LEVEL
FERTILITY LEVEL

FIG. 18. Dendrograph of relevés based on Gleason's modification of Jaccard's index of similarity.

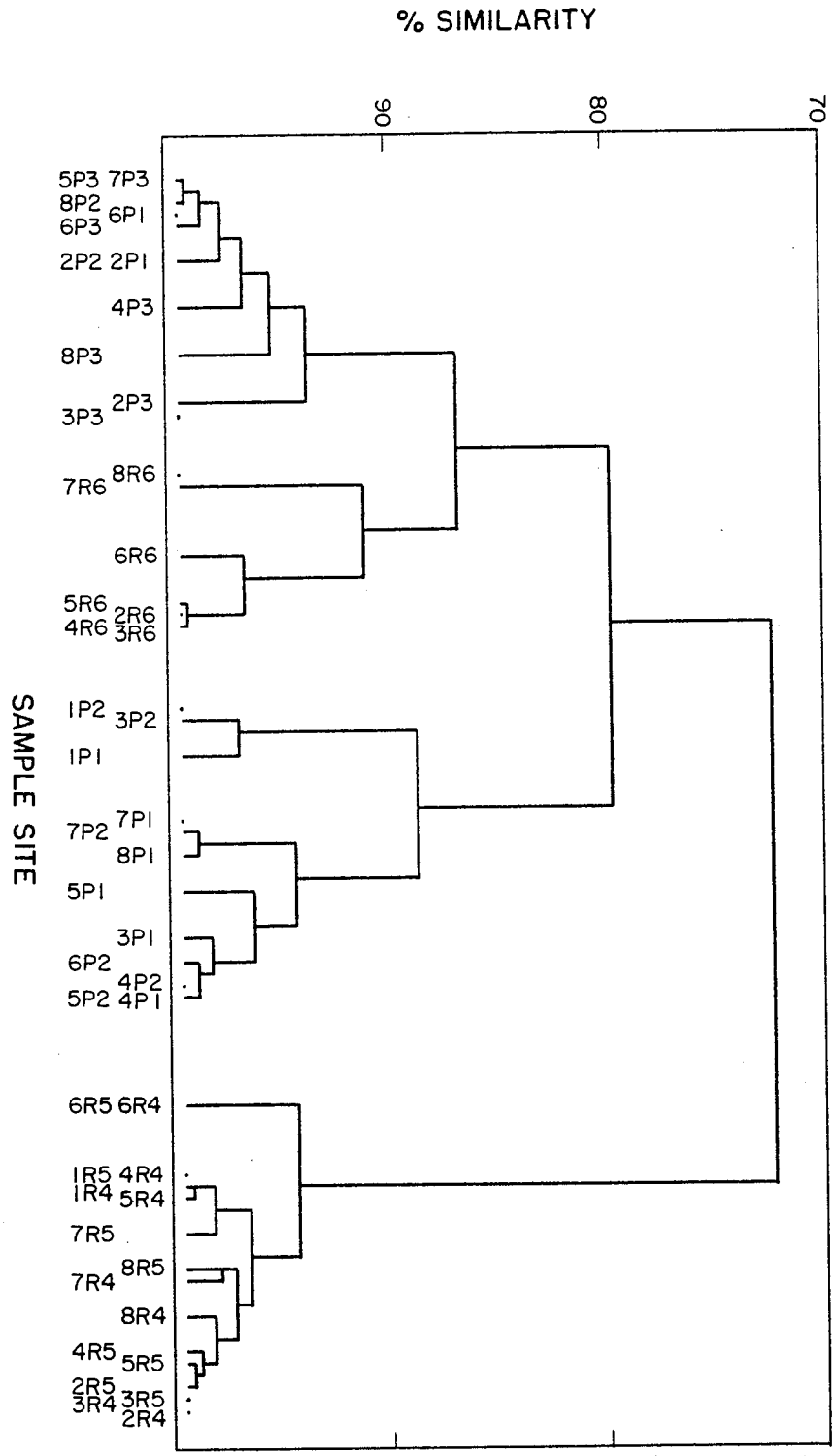

% SIMILARITY
90
80
70
SAMPLE SITE
5P3 7P3
8P2
6P3 6P1
2P2 2P1
4P3
8P3
3P3 2P3
7R6 8R6
6R6
5R6 2R6
4R6 3R6
1P2 3P2
1P1
7P2 7P1
8P1
5P1
3P1
6P2
4P2
5P2 4P1
6R5 6R4
1R5 4R4
1R4 5R4
7R5
7R4 8R5
8R4
4R5 5R5
2R5
3R4 3R5
2R4

FIG. 19. Dendrograph of relevēs based on Spatz's modification of Jaccard's index of similarity.

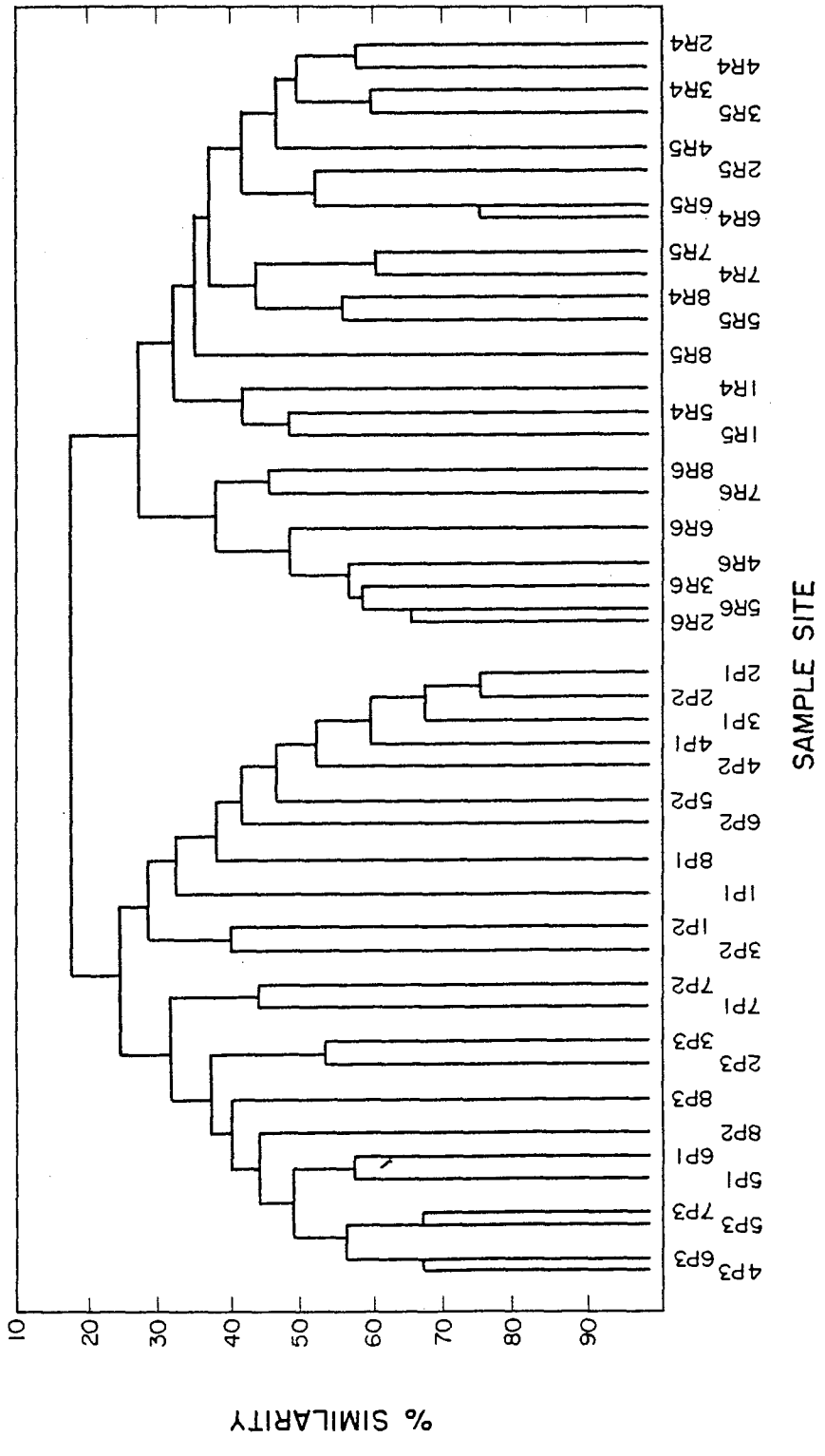
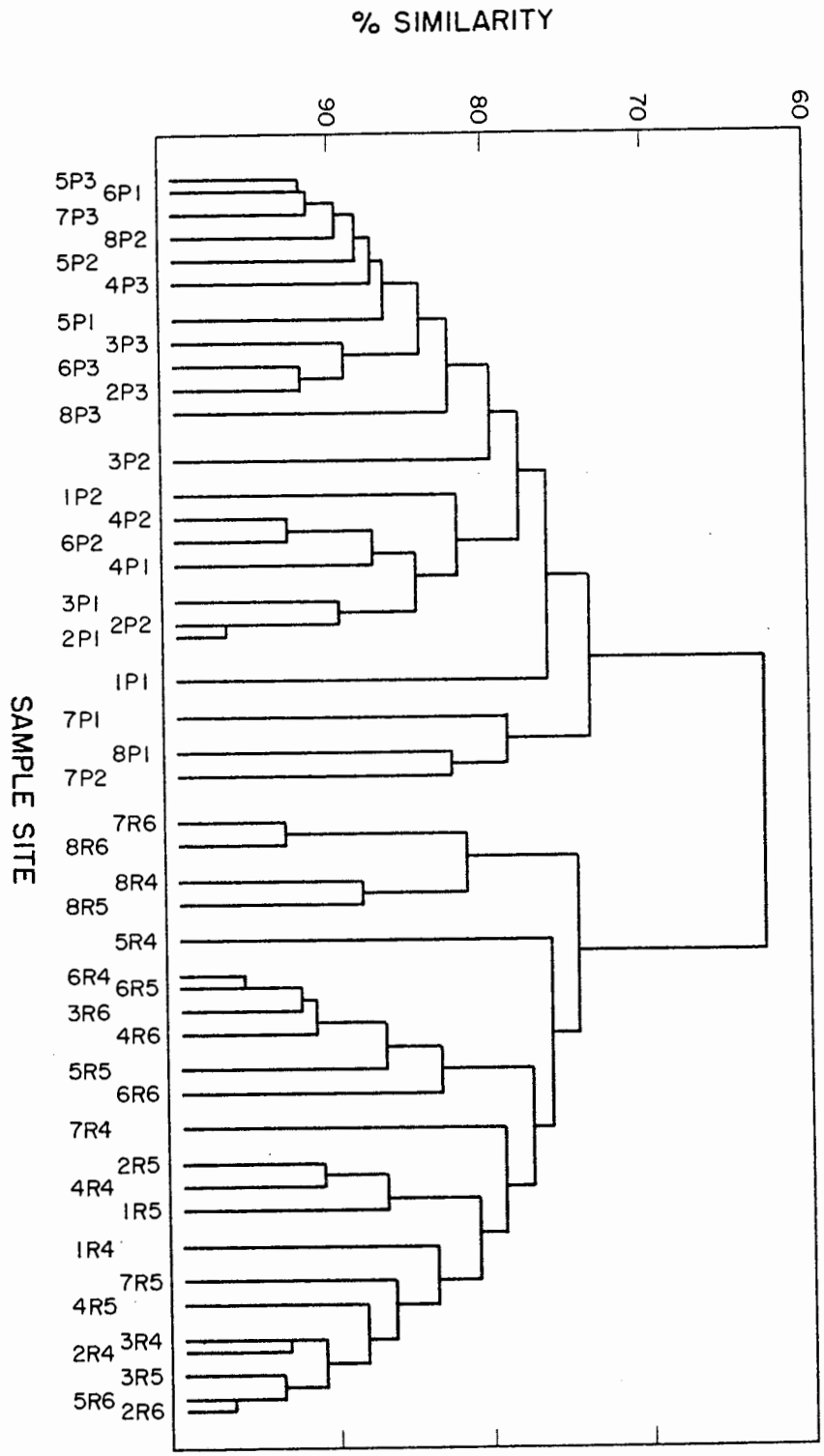

% SIMILARITY
10
20
30
40
50
60
70
80
90
SAMPLE SITE
4P3
6P3
5P3
7P3
5P1
6P1
8P2
8P3
2P3
3P3
7P1
7P2
3P2
1P2
1P1
8P1
6P2
5P2
4P2
4P1
3P1
2P2
2P1
5R6
2R6
3R6
4R6
6R6
7R6
8R6
1R5
5R4
1R4
8R5
5R5
8R4
7R4
7R5
6R4
6R5
2R5
4R5
3R5
3R4
4R4
2R4

FIG. 20. Dendrograph of relevēs based on Sorensen's index of similarity (presence/absence).


% SIMILARITY
90
80
70
60
SAMPLE SITE
5P3
6P1
7P3
8P2
5P2
4P3
5P1
3P3
6P3
2P3
8P3
3P2
1P2
4P2
6P2
4P1
3P1
2P2
2P1
1P1
7P1
8P1
7P2
7R6
8R6
8R4
8R5
5R4
6R4
6R5
3R6
4R6
5R5
6R6
7R4
2R5
4R4
1R5
1R4
7R5
4R5
3R4
2R4
3R5
5R6
2R6